CHARLES UNIVERSITY IN PRAGUE

Faculty of Science, Department of Ecology

Study programme: Ecology

Significance of predation for breeding ecology and conservation in shorebirds

Význam predace pro hnízdní ekologii a ochranu bahňáků

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Ph.D. Thesis

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Broken-wing display performed by American Golden Plover (*Pluvialis dominica*) near nest, Alaska, USA, 2012

Displaying male od Pectoral Sandpiper (*Cilidris melanotos*) in Barrow, Alaska, USA, 2012

CONTENTS

DECLARATION OF ORIGINALITY

I declare that this thesis has not been submitted for the purpose of obtaining the same or any other academic degree earlier or at another institution. My involvement in the research presented in this thesis is specified in the statement of contributions and it is also expressed through the authorship order of the included publications and manuscripts. All relevant literature sources used while writing chapters in this thesis have been properly cited. I am the author of all cover photographs presented through this thesis.

Vojtěch Kubelka

České Budějovice, Czech Republic, July 2018

STATEMENT OF CONTRIBUTION

This dissertation is the cumulative work based on productive collaboration with numerous scientists worldwide. My personal contribution to the conception, data collection, analysis, and writing of each of the following chapters is detailed below. All co-authors have seen relevant parts of this statement and have given their consensual agreement that my contributions are correct and that I may use these manuscripts in this dissertation.

Chapter 2

Kubelka V., Sládeček, M. & Šálek M. Great variability in the nest lining size: support for thermoregulation but not for anti-predatory adaptation hypothesis. (manuscript)
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Chapter 3

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Chapter 4

Zámečník V., **Kubelka V.** & Šálek M. 2018: Visible marking of wader nests to avoid damage by farmers does not increase nest predation. (*Bird Conservation International* 28: 293–301)
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Chapter 6

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Chapter 7

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Šálek M., Sládeček M., **Kubelka V.**, Mlíkovský J., Storch D. & Šmilauer P. Beyond habitat: spatial structure of nesting wetland bird community is determined by conspecific and heterospecific attraction. (manuscript before resubmission)
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Chapter 9

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Chapter 10

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Chapter 11

Kubelka V., Šálek M., Tomkovich P., Végvári Z, Freckleton R. & Székely T. Global pattern of nest predation is disrupted by climate change in shorebirds. (in revision)
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Chapter 12

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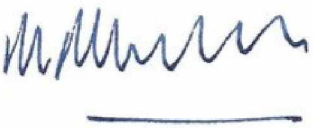

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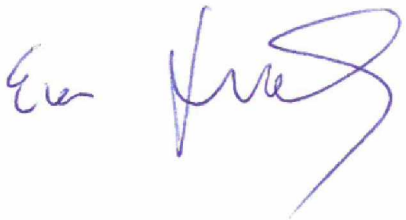

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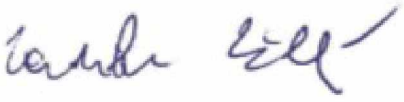

ABSTRACT

Predation is the most common cause of reproduction failure and it strongly influences breeding performance in birds, impacting the whole species population dynamics as well as it represents a major force in the evolution of avian life-history strategies. Investigating the factors driving predation rates, or quantifying predation consequences, is highly relevant for evolutionary ecology as well as for species conservation, especially in a rapidly changing world. In this dissertation, I investigate links between nest and chick predation, environmental factors, life-history and anti-predatory strategies, together with consequences for population dynamics and conservation. I use shorebirds as a uniquely suitable model system for three reasons: i) they are globally distributed; ii) have predominant ground nesting strategy and high interspecific similarity in nest appearance to potential predators; iii) are sufficiently well-studied in terms of nest predation all over the world.

In the two first sections of this dissertation, *Predation in the agricultural landscape* and *Interspecific interactions and anti-predatory strategies*, **Chapter 2** supports the thermoregulatory hypothesis of nest lining size rather than anti-predatory adaptation. **Chapter 3** discusses, from the perspective of predation, the twofold advantage for chicks hatched from bigger eggs earlier in the breeding season with better food availability. **Chapter 4** presents a finely tuned solution of how to effectively mark nests against agriculture machinery, but not attract predators at the same time. **Chapter 5** describes the current state of shorebirds in the Czech Republic and discuss the new agri-environmental scheme for Northern Lapwing on arable land, effectively promoting the whole biodiversity of the agricultural landscape. **Chapters 7** and **8** highlight the importance of anti-predatory "umbrella effect" of active nest defenders for timid species precipitating into the whole marshland bird community species composition, richness and abundance. On the contrary, **Chapter 9** questions the effectiveness of shorebird breeding associations with terns and reports high nest predation near Caspian Lake. Two chapters review peculiarities from shorebird breeding (nest scrape reuse, **Chapter 6**) and foraging ecology (inter and intraspecific predation among shorebirds, **Chapter 10**).

In the last section, *Global perspectives on nest predation*, nest predation patterns are examined from large spatial and temporal perspectives with the use of 38,191 nests from 237 populations in 111 shorebirds species over 149 localities across all continents, covering the time span of last 70 years. There are three main novel outputs from **Chapter 11**: i) the first global evidence for the latitudinal gradient in offspring predation of wild populations with the highest historic predation rates in the tropics; ii) an extremely rapid increase in nest predation recorded in the North temperate region and especially in the Arctic recently, rendering these breeding grounds an extensive ecological trap for migratory shorebirds; iii) a revealed link between climate change and nest predation rates, thus demonstrating a global-scale impact of climate change on trophic interactions between predators and prey. Furthermore, climate change and life-history traits impact on population dynamics (**Chapter 12**), biparental incubation reduces nest predation rates and nest predation is the significant predictor of population dynamics in shorebirds (**Chapter 13**). Shorebirds are declining globally, therefore further disentangling and relevance assessment of particular factors driving population dynamics of shorebirds is urgently needed and precipitation of these findings into conservation practice essential to secure future for our admirable shorebirds.

ABSTRAKT

Predace je nejčastější příčinou reprodukčního neúspěchu a silně ovlivňuje hnízdní produktivitu a celkovou populační dynamiku ptáků. Zároveň významně ovlivňuje evoluci jejich životních strategií. Výzkum faktorů ovlivňujících míru predace a kvantifikace následků predace jsou velmi významné z pohledu evoluční ekologie i druhové ochrany, zejména v současně se rychle měnícím světě. V této dizertační práci řeším vztahy mezi: mírou predace hnízd nebo kuřat, environmentálními faktory a životními strategiemi, vše společně s následky pro populační dynamiku a ochranu přírody. Skupina bahňáků představuje vhodný modelový systém ze třech důvodů: 1) bahňáci jsou rozšířeni celosvětově; 2) hnízdí převážně na zemi a jejich hnízda mají mezidruhově velmi podobný vzhled pro potenciální predátory; 3) hnízdní predace u bahňáků je dostatečně prostudována napříč celým světem.

V rámci dvou částí této dizertační práce, *Predace v zemědělské krajině* a *Mezidruhové interakce a anti-predační strategie*, podporujeme termoregulační hypotézu velikosti hnízdní výstelky, nikoliv však anti-predační adaptaci (**Kapitola 2**). Dále z predační perspektivy diskutujeme dvojitou výhodu kuřat vylíhnutých z větších vajec na začátku hnízdní sezóny s větším množstvím dostupné potravy (**Kapitola 3**). Představujme vhodné řešení, jak efektivně značit hnízda před zničením zemědělskou technikou a přitom nezvyšovat riziko predace hnízd (**Kapitola 4**). Popisujeme současnou situaci bahňáků v České republice a diskutuje nové agro-environmentální opatření pro čejku chocholatou na orné půdě, které podporuje celkovou biodiverzitu zemědělské krajiny (**Kapitola 5**). Zdůrazňujeme význam anti-predačního „ochranného deštníku" aktivních obránců pro neagresivní druhy a jeho důsledky pro celkové druhové složení a bohatost mokřadního společenstva ptáků (**Kapitoly 7** a **8**). Dokládáme vysokou míru predace hnízd bahňáků ve stepi poblíž Kaspického moře (**Kapitola 9**). Shrnujeme zajímavosti z hnízdní biologie bahňáků – opětovné využívání hnízdních důlků (**Kapitola 6**) a z jejich potravní ekologie – mezi a vnitrodruhová predace mezi bahňáky (**Kapitola 10**).

V poslední části, *Globální perspektivy hnízdní predace*, jsou patrnosti hnízdní predace podrobeny výzkumu v rozsáhlém prostorovém a časovém měřítku s využitím 38 191 hnízd, 237 populací, 111 druhů bahňáků na 149 lokalitách napříč všemi kontinenty v rozmezí posledních 70-ti let. Prezentujeme tři zásadní výstupy z **Kapitoly 11**: 1) první globální důkaz pro latitudinální gradient v predaci potomstva divoce žijících populací s nejvyšší historickou mírou predace v tropech; 2) velmi rychlý nárůst predace hnízd zaznamenaný na severu v zóně mírného pásu a zejména v Arktidě; 3) vztah mezi klimatickou změnou a hnízdní predací demonstrující vliv klimatické změny na potravní interakce mezi predátory a kořistí na globální škále. Následuje kapitola, kde popisujeme vliv klimatické změny a životních strategií na populační dynamiku (**Kapitola 12**) Dále jsme zjistili, že biparentální inkubace snižuje hnízdní predaci a že hnízdní predace je významným prediktorem populační dynamiky bahňáků (**Kapitola 13**). Bahňáci celosvětově ubývají, proto je nezbytný další výzkum a odhad relativního vlivu jednotlivých faktorů určujících populační dynamiku bahňáků, společně s přenesením vědeckých poznatků do ochranářské praxe pro zachování jedinečných bahňáků.

Grey-breasted Seedsnipe (*Thinocorus orbignyianus*) in Andean Altiplano, altitude of 4 450 m., Peru, 2017

Chapter 1

Introduction

Vojtěch Kubelka

In this dissertation, I explore the relationship between predation and reproduction using shorebirds as model organisms. First, I explain the significance of each of these components, and then describe the connectivity between them and put my dissertation's chapters into their context. I end up the Introduction with the outline and structure of this thesis.

Why predation?

Predation is the most probable fate for a large proportion of organisms upon Earth (Sih *et al.*, 1985; Polis *et al.*, 1989; Lima & Dill, 1990; Barbosa & Castellanos, 2005). From evolutionary perspective the never-ending arms race "to eat but not being predated" (Dawkins & Krebs, 1979) has shaped some of the most spectacular morphological adaptations and interesting complex behaviours in the animal kingdom (Lima, 1998; Caro, 2005), such as in the extreme the offspring protection and development in the stomach of two, now sadly extinct, species of gastric-brooding frogs (Corben *et al.*, 1974; McDonald & Tyler, 1984); or, from the predator's point of view, the diverse hunting strategies of Killer Whales (*Orcinus orca*) with high level of co-operation among these hunters, and their prey ranging from fish, birds, sea lions to other whales (Lopez & Lopez, 1985; Pitman & Ensor, 2003). Predation acts in every corner of our planet and extreme rates of predation can quickly lead to species extinction (Bennett & Owens, 2002; Blackburn *et al.*, 2004). Investigating the factors that influence predation rates, or quantifying predation consequences, is highly relevant for evolutionary ecology as well as for species conservation (Ritchie & Johnson, 2009).

Why reproduction and predation?

Predation is the most common case of reproduction failure (e.g. Ricklefs, 1969; Bailey & Houde, 1989; Martin, 1993; Thompson, 2007) and it strongly influences overall breeding performance in birds (Skutch, 1949; Lack, 1966), where open nests with eggs or freely foraging precocial chicks are highly exposed to potential predators (Starck & Ricklefs, 1998; Bennett & Owens, 2002). Predation is thus inevitably impacting the whole species population dynamics (Evans & Pienkowski, 1984; Bennett & Owens, 2002; Colwell, 2010). Because every bird experiences predation risk, predation shapes avian life-history traits associated with breeding such as nest construction, clutch size or anti-predatory tactics (Gochfeld, 1984; Martin, 1995; Gill, 2007; Cresswell, 2008; Lima, 2009; Biancucci & Martin, 2010; Mainwaring *et al.*, 2015). There are many well-explored links among life-history strategies, predation and environmental factors (further described in detail), but major knowledge gaps still remain to be investigated (MacDonald & Bolton, 2008; Roper *et al.*, 2010; Brawn *et al.*, 2011; Ibáñez-Álamo *et al.*, 2015; Mainwaring *et al.*, 2015). Better understanding of causes and consequences of predation rates is even more important now, in rapidly changing word (Tylianakis *et al.*, 2008; Gilg *et al.*, 2012; Scheffers *et al.*, 2016), especially in the light of current concerns about rapid increase of nest and offspring predation rates in Europe, North America or Australia (Remeš *et al.*, 2012; Roodbergen *et al.*, 2012; Munro, 2017).

Why shorebirds, reproduction and predation?

I consider shorebirds that represent 245 species from 16 families (table 1) classified into the order Charadriiformes (del Hoyo & Collar, 2014; Gill & Donsker, 2016; del Hoyo *et al.*, 2018). I exclude gulls, terns and auks, which is reasonable from the perspective of eco-morphological coherence of the focal species (del Hoyo *et al.*, 2018). Shorebirds (plovers, sandpipers and allies) represent a unique group of birds and excellent study organisms for several reasons.

First, many shorebirds are migratory species individually encompassing several continents, and they exhibit some of the best studied migratory behaviours of all organisms (Alerstam *et al.*, 2001; Kvist *et al.*, 2001; Delany *et al.*, 2009; Colwell, 2010). They are not only flying the longest non-stop flights, more than 10,000 km in the case of the Bar-tailed Godwit (*Limosa lapponica*) wintering in New Zealand (Gill *et al.*, 2009; Battley *et al.*, 2012), but for example males of Pectoral Sandpiper (*Calidris melanotos*) can fly more than 13,000 km in total during one short summer when pursuing females at the many Arctic breeding grounds, and this all happens after exacting migration from Southern hemisphere (Kempenaers & Valcu, 2017). One of the reasons for these remarkable journeys could be an exploitation of presumed lower predation pressure high in the Arctic (McKinnon *et al.*, 2010).

Second, shorebirds live in every biome on the Earth (Fig. 1) inhabiting all main terrestrial habitats. Although predominantly living near shorelines and in various types of marshlands, they can breed in rainforests as well as in deserts, in both polar regions as well as in high mountains – e.g. the harsh Andean Antiplano in elevation more than 4,000 m is inhabited by several endemic shorebird species including herbivorous Seedsnipes (Thinocoridae). Shorebirds can find their home in the vast steppes as well as on remote atolls in the Pacific (Hayman *et al.*, 1986; BirdLife International, 2018; del Hoyo *et al.*, 2018). Many species also breed in a human-created environment and they can suffer high nest and chick predation rates in intensively cultivated agricultural landscapes (e.g. Roodbergen *et al.*, 2012; Kentie *et al.*, 2015; Laidlaw *et al.*, 2017).

Third, there are many extraordinary and diverse reproductive strategies evolved by shorebirds that have been used extensively to test evolutionary theories of life histories, sexual selection and adaptation (Thomas *et al.*, 2007; Lesku *et al.*, 2012; Liker *et al.*, 2013; Eberhart-Phillips *et al.*, 2018). For example, we can find several independent origins of sex-role reversal in shorebirds, where females compete for mates and males perform all incubation and chick rearing care (del Hoyo *et al.*, 2018) and this sex-role reversal is related to adult sex ratio in shorebirds populations (Liker *et al.*, 2013). An interesting mating tactic is demonstrated by Temminck's Stint (*Calidris temminckii*) which usually performs rapid double-clutching: a female lays two clutches with two males in quick succession of several days and one is cared by the female and one by a male (Hilden, 1975). Quite surprisingly, Southern Lapwing (*Vanellus chilensis*) can breed cooperatively (Walters & Walters, 1980) and when doing so, lapwings can lower their nest predation rates (Santos & Macedo, 2017). Uniquely in the bird kingdom, Crab-plover (*Dromas ardeola*) use solar energy to incubate: unusually among shorebirds they breed in sand dune dens protected from predators and leave one white egg to be predominantly incubated by hot Arabic sun (De Marchi *et al.*, 2008).

Fourth, shorebirds are ideal ecological indicator species for the quality of a diverse array of wetland and agricultural habitats (e.g. Atkinson *et al.*, 2006; Butler *et al.*, 2007; Reif *et al.*, 2008; Delany *et al.*, 2009; Kamp *et al.*, 2011; Sutherland *et al.*, 2012; Amano *et al.*, 2018). Importantly from a conservation perspective, many shorebird species are declining (Munro, 2017; Studds *et al.*, 2017; BirdLife International, 2018) with some charismatic species facing the imminent threat of extinction: e.g. Spoon-billed Sandpiper (*Calidris pygmaea*) in remote Chukotka (Clark *et al.*, 2018) or Slender-billed Curlew (*Numenius tenuirostris*) lost in south-west Siberia (Kirwan *et al.*, 2015).

In this dissertation I investigate nest predation in shorebirds. Three features of shorebirds make them uniquely suitable for such analysis: i) they are globally distributed; ii) have predominant ground nesting strategy and high inter-specific similarity in nest appearance to potential predators; iii) are sufficiently well-studied in terms of nest predation all over the world (Cramp & Simmons, 1983; Urban *et al.*, 1986; Marchant & Higgins, 1993; Higgins & Davies, 1996; MacDonald & Bolton, 2008; Colwell, 2010; Roodbergen *et al.*, 2012; Poole, 2015; BirdLife International, 2018; del Hoyo *et al.*, 2018).

Table 1. Shorebird families with the number of species in given family. Gulls, terns and auks are excluded due to the better eco-morphological coherence of the focal 245 species.

Family	No. of species	Family	No. of species
Thick-knees and Stone Curlews (Burhinidae)	10	Sheathbills (Chionidae)	2
Magellanic Plover (Pluvianellidae)	1	Egyptian Plover (Pluvianidae)	1
Oystercatchers (Haematopodidae)	9	Ibisbil (Ibidorhynchidae)	1
Stilts and avocets (Recurvirostridae)	7	Plovers (Charadriidae)	71
Plains-wanderer (Pedionomidae)	1	Seedsnipes (Thinocoridae)	4
Painted-snipes (Rostratulidae)	3	Jacanas (Jacanidae)	8
Sandpipers and Snipes (Scolopacidae)	91	Buttonquails (Turnicidae)	18
Crab-plover (Dromadidae)	1	Coursers and Pratincoles (Glareolidae)	17

Factors influencing nest and chick predation in shorebirds

I have not intended this section of the dissertation as an exhaustive review of all possible factors influencing nest or chick predation in shorebirds. It represents rather a selection of the most important factors with direct relevance to the studies presented in this dissertation, mainly targeted on the nest predation. Generally, we can distinguish: 1) *intrinsic factors*, inherent to shorebirds themselves, the anti-predatory strategies in our case (e.g. Gochfeld, 1984); and 2) *extrinsic factors*, which are predominantly acting independently from shorebirds themselves, for instance driven by environmental conditions such as the variability and abundance of predators (e.g. MacDonald & Bolton, 2008; DeGregorio *et al.*, 2016). Further external factors can affect predation rates indirectly via changed behaviour of predators, changed predator communities, or breeding habitat quality (e.g. Schlaepfer *et al.*, 2002; Meltofte *et al.*, 2007; Gilg *et al.*, 2012), and not surprisingly, human impact can be negative as well as positive (e.g. Colwell, 2010). Some of the factors of interest are very

difficult or even impossible to obtain, for example, the full predator species composition and their relative nest predation importance for all investigated shorebirds populations. But owing to the gradual transition of predator communities with ecosystem changes over large terrestrial land masses (DeGregorio *et al.*, 2016), latitude, in this case, can be used effectively as a synoptic variable (Ricklefs, 1969; Stutchbury & Morton, 2001). We will focus on selected important factors influencing nest and chick predation of shorebirds in more detail in the following paragraphs.

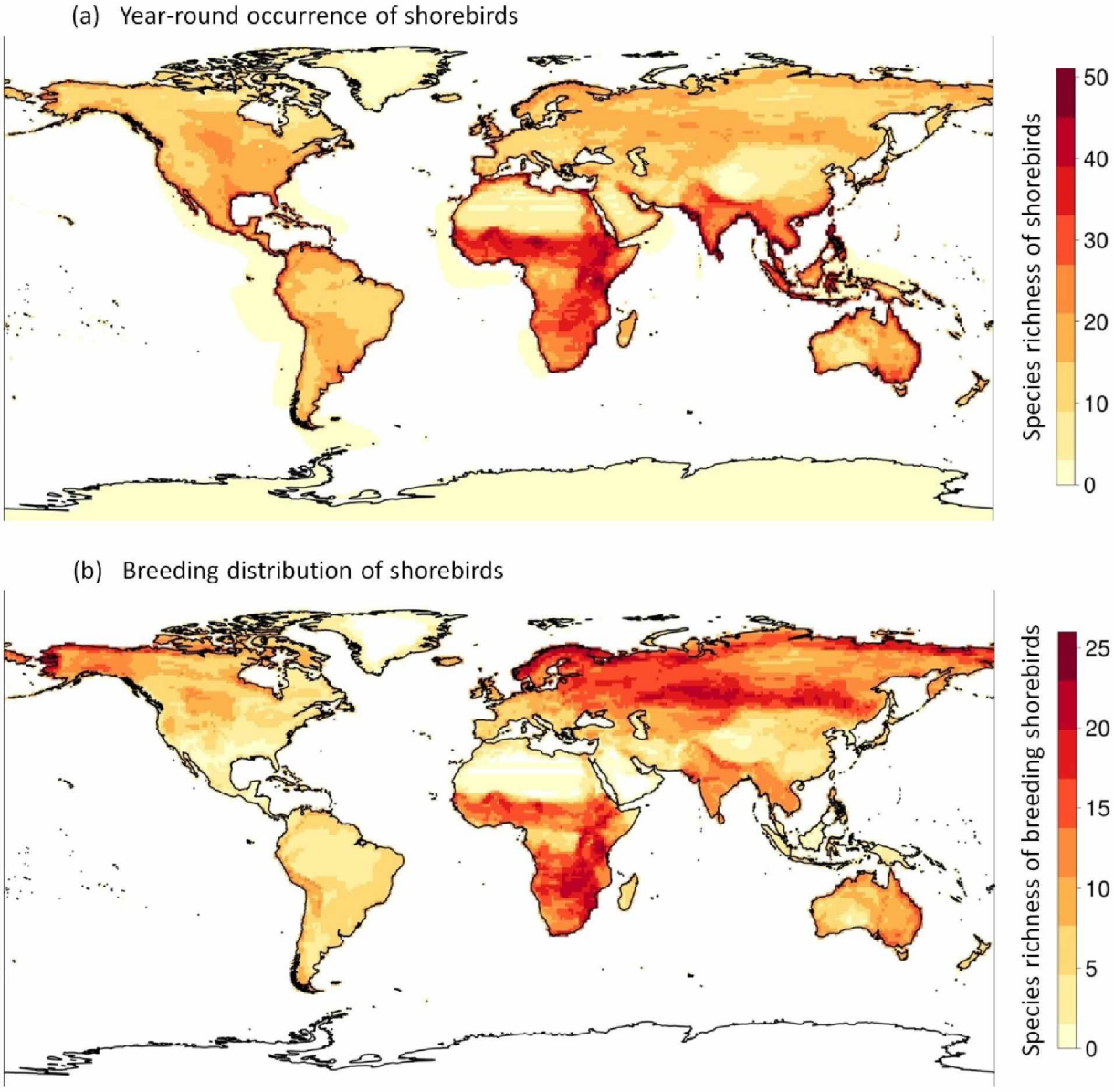

Figure 1. Global distribution of shorebirds. **(a)** Year-round / through the whole year occurrence – regular breeding or passage or non-breeding occurrence or their combination. **(b)** Breeding distribution – the species is known or thought very likely to occur regularly during the breeding season and to breed. Data are adapted from Bird species distribution maps of the world at the one-degree spatial resolution (BirdLife International, 2018). Data are presented for 245 species of shorebirds (table 1). Maps preparation credits: Anna Tószögyová.

Anti-predatory strategies

Among bird groups, shorebirds demonstrate the most spectacular diversity of anti-predatory strategies during breeding (Gochfeld, 1984; Walters, 1990; Larsen, 1991; del Hoyo *et al.*, 2018), altogether accounting for at least 20 tactics which we can group according to time of occurrence and behaviour similarity (table 2).

Table 2. Nest anti-predatory strategies adopted by shorebirds. Adapted according to Gochfeld (1984), where detailed delineations are available. Recently recognized strategies are marked with * and their brief description follows in the text. Many of these strategies are also performed during the chick-rearing period of shorebirds.

Category	Group	#	Strategy (tactic)	Notes, species
Eco-behavioural - in advance	Nest placement and visibility	1	Nest and egg crypsis	all shorebirds except Crab Plover
		2	Nest in trees; roof breeding *	six sandpipers; two lapwings
		3	Hidden nest in burrow *	Crab Plover, Shore Plover
		4	Nest concealment	mainly family Scolopacidae
		5	Saver area - latitude, islands *	different scales, many species
		6	Small clutch size *	tropical, South temperate species
	Help of others	7	Helpers *	Southern Lapwing
		8	Coloniality, breeding density	vs. spacing out, many species
		9	Protective umbrella	several timid species
Behavioural - upon predator's approach	Flee + distant alarm or hide	10	Early surreptitious departure	also fly away trick
		11	Covering eggs with upon departure	thermoregulation function too
		12	Call from distance	vs. stay silent, many species
	Distraction	13	Sitting tight	also background matching
		14	Distraction display, "injured" adult	"broken" wing etc., rodent run, ...
		15	Displacement activities	false brooding, feeding, ...
	Mate guarding	16	Guarding next to incubating mate *	many biparental species
	Aggressiveness	17	Ungulate display	lapwings, some plovers
		18	Snake pecking *	at least two lapwings
		19	Aggressive circling and scolding	many species
		20	Attacking	aggressive, bigger species

The first category consists of eco-behavioural adaptations preceding the imminent threat of predator presence in the vicinity of eggs or chicks. Nest placement and visibility represent an obvious group of anti-predatory tactics. For example nest and egg crypsis is successfully adopted by nearly all shorebirds (Gochfeld, 1984; Colwell, 2010; del Hoyo *et al.*, 2018). Since many articles have been written about shorebird egg crypsis itself (Nguyen *et al.*, 2007; Pereira & Amat, 2010; Stevens, 2011; Skrade & Dinsmore, 2013; Gómez *et al.*, 2016; Troscianko *et al.*, 2016), less attention have been given to the nest lining conspicuousness and

its size in relation to predation (Solís & De Lope, 1995; Mayer *et al.*, 2009; Colwell *et al.*, 2011). Here, we address this issue in **Chapter** 2 focusing on factors influencing variability in nest lining magnitude in Northern Lapwing (*Vanellus vanellus*) and consequences for nest predation. Furthermore, considering nest visibility to predators from the conservation perspective, in **Chapter 4**, we try to find an optimal way of nest marking against damage by agriculture machinery which would not attract potential predators at the same time. Although direct nest protection can work well, well-targeted agri-environmental schemes could be more efficient at larger scales (Ottvall & Smith, 2006; Verhulst *et al.*, 2007; Schmidt *et al.*, 2017) and we discuss the best conservation approaches in **Chapter 5**.

Nest placement from broader perspective includes searching for safer areas to breed with lower predation pressure. Generally, higher latitudes are perceived as safer locations for breeding (McKinnon *et al.*, 2010), and we test this assumption in **Chapter 11**. See more details in *Diversity of predators, latitudinal gradient* paragraphs below. However, also breeding on offshore islands with limited access for ground predators, at the lake islands or in river deltas with many channels can be perceived as anti-predatory strategy (Clark & Shutler, 1999) exploited by many shorebird species (e.g. Cramp & Simmons, 1983; del Hoyo *et al.*, 2018). On the finer scale of nesting habitat selection, unusually among shorebirds, next to the Crab Plover, also Shore Plover (*Thinornis novaeseelandiae*) hide its nest, in this case in cavities among boulders (del Hoyo *et al.*, 2018). On the other hand, three species: Green Sandpiper (*Tringa ochoropus*), Solitary Sandpiper (*Tringa solitaria*) and Nordmann's Greenshank (*Tringa guttifer*) predominantly breed in trees in old nests of song birds or build their own nest from twigs in the case of Nordmann's Greenshank (Cramp & Simmons, 1983; del Hoyo *et al.*, 1996). Usage of old songbird nests, mainly trushes (*Turdus* ssp.) in trees is sometimes performed by Grey-tailed Tattler (*Tringa brevipes*) or Wood Sandpiper (*Tringa glareola*) as well (Pulliainen & Saari, 1991; del Hoyo *et al.*, 1996). Also Tuamotu Sandpiper (*Prosobonia parvirostris*) breeding at remote atolls in Pacific can sometimes place the nest to the tree (D. Lank *in litt.*). Red-wattled Lapwings (*Vanellus indicus*) have been shown to make profit from artificial structures and perform nesting on building roofs or walls in India (e.g. Tehsin & Lokhandwala, 1982; Shangha, 2011; Muralidhar & Barve, 2013), where according to expectation, nest predation is indeed lower for roof nests in comparison with nests placed normally on the ground (Sethi *et al.*, 2011).

Despite the fact that some shorebirds as Jacanas or Kitlitz's Plover (*Charadrius pecuarius*) can move the location of their nest and clutch during incubation, possibly also as anti-predatory reaction (del Hoyo et al., 2018), chick transfer performed by Jacanas or Eurasian Woodcock (*Scolopax rusticola*) is perceived as distinct anti-predatory strategy (e.g. Cramp & Simmons, 1983; del Hoyo et al., 2018). Another generally widespread phenomenon among shorebirds, enhancing performance of precocial chicks, is relatively bigger egg size in comparison with altricial birds (Rahn *et al.*, 1975; Starck & Ricklefs, 1998; Deeming, 2002). Heavier chicks from bigger eggs are in better condition, they can forage longer and they can more easily escape from predators in comparison with smaller conspecifics (Davis, 1975; Galbraith, 1988; Bolton, 1991; Grant, 1991; Blomqvist *et al.*, 1997; Sheldon, 2002; Evans, 2004). In **Chapter 3**, we discuss factors influencing the egg size variation with consequences for chick predation in Northern Lapwing. Apart from the egg size, another type of maternal

investment can be the clutch size. Despite the fact that shorebirds lay predominantly invariant clutch of four eggs (Arnold, 1999), the variability in mean clutch size among species exists (Maclean, 1972) and therefore in **Chapter 13**, we discuss whether mean clutch size in shorebirds corresponds with other bird groups shoving smaller clutch sizes in tropics as a presumable response to higher predation pressure (Lima, 1987; Arnold, 1999).

Another group of eco-behavioural anti-predatory adaptations involving nest placement decision consists of help from other birds, namely colonial breeding or in timid species – seeking for anti-predatory "protective umbrella" from bold aggressive species – the active nest defenders (Bub, 1957; Nankinov, 1978; Dyrcz *et al.*, 1981; Larsen & Moldsvor, 1992; Hegyi & Sasvári, 1997; Powell, 2001; Šálek & Šmilauer, 2002; Nguyen *et al.*, 2006; Sládeček *et al.*, 2014; Kubelka *et al.*, 2014; del Hoyo *et al.*, 2018). These breeding associations are generally assumed to be successful anti-predatory strategies (Haemig, 2001; Quinn & Ueta, 2008). However, there are possible drawbacks when such associations are effectively exploited by predators (Caro, 2005; McKinnon *et al.*, 2013; Giroux *et al.*, 2016). Because costs and benefits of breeding associations for protective and protected species are still not fully understood (Quinn & Ueta 2008), we target this issue in series of four **Chapters 6–9** under different environmental conditions and species composition. The special case of interaction among shorebirds, inter and intraspecific predation is reviewed in **Chapter 10**.

The second category of shorebirds anti-predatory strategies encompasses various behavioural tactics in the close presence of potential predator threatening nest or chicks. Various escape tactics are well known and described (e.g. Cramp & Simmons, 1983; Gochfeld, 1984; del Hoyo *et al.*, 2018). More finer division of several special cases of distraction displays, e.g. showing a nest of nearby nesting tern by plover to an approaching predator rather than revealing position of its own nest (Gochfeld, 1984) seems to me as not justifiable, because it involves too much of anthropomorphic explanation. We can view the guarding (staying nearby) of the incubating mate as a separate anti-predatory strategy of biparental shorebird species with several advantages including an early warning or a help with deterring of potential predators from the breeding site (Larsen *et al.*, 1996). We test the anti-predatory advantage of this behaviour in **Chapter 13**. Among well-known shorebird aggressive behaviour categories such as direct physical attack of birds and mammals or the ungulate display (e.g. Gochfeld, 1984; Larsen *et al.*, 1996), we can define another distinct category, the "reptile pecking" or "pecking attack", described for Southern Lapwing in Venezuela during chick-rearing (Walters, 1990) and for Senegal Lapwing (*Vanellus lugubris*) in Gabon during incubation period (Mibambani et al., 2009). This behaviour consists of wings stretched specifically out to the side, facing the reptile and active pecking accompanied by characteristic vocalisation (Walters, 1990; Mibambani et al., 2009). In the second case, lapwings were able to pick up and drop the snake repeatedly to finally relocate it away from the nest (Mibambani *et al.*, 2009). Given the relative importance of snakes as bird nest predators in the tropics (Skutch, 1985; Weatherhead & Blouin-demers, 2004; Robinson *et al.*, 2005), it is probable that such behaviour can be present, but so far overlooked, in other tropical lapwings or other shorebirds.

Diversity of predators and latitudinal gradient

Life-history theory and regional empirical evidence predict that nest predation rates should be higher in the tropics than in temperate and arctic regions (Skutch, 1949; Ricklefs, 1969; Stutchbury & Morton, 2001; Griebeler *et al.*, 2010; Roper *et al.*, 2010). The higher diversity of nest predators in the tropics (Ricklefs, 1969), particularly snakes (Skutch, 1985; Weatherhead & Blouin-demers, 2004; Robinson *et al.*, 2005) or small mammals (Roper & Goldstein, 1997), is supposed to be primarily responsible for higher nest predation rate near the equator. This assumption was demonstrated in North America, but only from temperate to arctic regions (DeGregorio *et al.*, 2016).

The latitudinal nest predation hypothesis has received scattered supporting evidence from several local studies with high nest predation rate in tropical regions (e.g. Marchant 1960; Skutch 1966; Mezquida & Marone 2001; Stutchbury & Morton 2001; Lloyd 2004) or low predation in the sub-Arctic and Arctic (Ricklefs, 1969; Jehl Jr., 1971). Moreover, an experiment with artificial nests from sub-Arctic to High Arctic regions in Canada supported this pattern (McKinnon *et al.*, 2010), though artificial nest design could not reflect real predation rate (Wilson *et al.*, 1998; Zanette, 2002; Faaborg, 2010; Mainwaring *et al.*, 2015). Predation rates on real nests can be significantly affected by anti-predatory tactics of particular bird species (Gochfeld 1984; Weidinger 2002; Caro 2005). The latitudinal nest predation hypothesis has been tested and supported at broader geographical scale and larger sample sizes of real nests only with use of predominantly passerine species suffering from high heterogeneity in nest placement, nest size and clutch size (Ricklefs, 1969; Remeš *et al.*, 2012; DeGregorio *et al.*, 2016). These factors meaningfully influence nest predation (Kulesza, 1990; Martin, 1995; Robinson *et al.*, 2000; Biancucci & Martin, 2010) and they can become a reason for ambiguous latitudinal gradient (Martin, 1995).

The results of some studies are not in concordance with the latitudinal nest predation hypothesis (Marchant, 1960; Oniki, 1979; Robinson *et al.*, 2000) and it is still questioned (Brawn *et al.*, 2011). The majority of aforementioned studies lack phylogenetic correction and do not distinguish nest predation at egg and nestling stage, which can differ a lot in terms of predation (Auer *et al.*, 2007; Brawn *et al.*, 2011). Despite decades of research, latitudinal differences in life-histories or demographic parameters remain poorly understood (Roper *et al.*, 2010) and there is the need for more complex investigation of the latitudinal nest predation hypothesis that controls for phylogeny (Martin, 1996; Brawn *et al.*, 2011).

Here we address this major knowledge gap by a performance of a global spatial analysis on nest predation rates with use of 237 shorebird populations and the focus on the latitudinal gradient in nest predation (**Chapter 11**). Next steps and further implications for future research directions are discussed in **Chapter 13**.

Climate change

Climate change, more pronounced in the Arctic, can impact on breeding shorebirds in several ways (Meltofte *et al.*, 2007; Gilg *et al.*, 2012). Despite a possible short-term advantage of warmer temperatures for the breeding productivity of Arctic shorebirds (Meltofte *et al.*, 2007;

Weiser *et al.*, 2018), the greater the impact of climate change over the years at a given location, the bigger negative impact on species and biotic interactions is expected (Parmesan, 2006; Durant *et al.*, 2007; Gilg *et al.*, 2012). From perspective of predation, climate change can induce a mismatch between the hatching period in shorebirds and the peak of arthropod abundance during short Arctic summer (Durant *et al.*, 2007; Gilg *et al.*, 2012; van Gils *et al.*, 2016; Saalfeld & Lanctot, 2017). Thus weaker starving chicks could be easier prey for predators (Evans, 2004). Moreover, the current range expansion of several predators toward North, e.g. Red Fox (Gallant *et al.*, 2012) or Brown Bear (P. Tomkovich *in litt.*), can impose even higher predation pressure on nests of Arctic shorebirds.

Furthermore, lemmings, small rodents representing the key component of the Arctic food web, have experienced a crash in their abundances and population cyclicity due to unsuitable snow cover mediated by global warming (Ims *et al.*, 2008; Kausrud *et al.*, 2008; Aharon-Rotman *et al.*, 2014). The plight of lemmings was documented over vast Arctic areas just prior to the year 2000 (Ims *et al.*, 2008; Kausrud *et al.*, 2008; Aharon-Rotman *et al.*, 2014) and these alterations in predator-prey interactions probably resulted in higher predation pressure on ground-nesting birds, well known alternative prey for Arctic predators – predominantly foxes and skuas (Meltofte *et al.*, 2007; Aharon-Rotman *et al.*, 2014; Mckinnon *et al.*, 2014). In **Chapter 11** we address this problem together with global temporal changes in nest predation and we test whether the current Arctic represents a large-scale ecological trap for migratory shorebirds from nest predation perspective.

Human disturbance and conservation measures

Humans occupy the same habitats as shorebirds at many occasions, and human negative impact can range from accidental crushing of eggs on the beach to extensive reclamation projects of intertidal mudflats and the loose of whole important staging area for migrating shorebirds with detrimental consequences for population trends (e.g. Colwell, 2010; Sutherland *et al.*, 2012; Piersma *et al.*, 2016). It is not surprising that many, mainly tropical shorebirds, are more or less harvested by local people for food (del Hoyo *et al.*, 2018), but e.g. egg collection can have a long tradition also in Western European countries (e.g. Both *et al.*, 2005). Agricultural landscapes represent suitable breeding environment for shorebirds (Hötker, 1991) but with many ecological traps (Schlaepfer *et al.*, 2002), including direct nest damage by agriculture machinery during field cultivation in the middle of shorebird incubation period or rendering particular habitats more susceptible to nest predation (e.g. van Der Wal & Palmer, 2008; Wilson *et al.*, 2009). Agriculture intensification can lead to indirect and far-reaching negative effects such an example of rapidly growing population of Arctic-breeding geese, especially Lesser Snow Geese (*Chen caerulescens caerulescens*) over recent decades due to changes in agriculture practices (Abraham *et al.*, 2005; Koons *et al.*, 2014) with already detected significant impact on the Arctic ecosystems (Flemming *et al.*, 2016). Predation on shorebirds nests has been raised via direct disturbance of incubating birds by grazing geese and subsequent predation or rendering shorebirds nests more obvious for predators in overgrazed short vegetation (Munro, 2017).

On the other hand, many people do their best to protect shorebirds and their habitats, in activities ranging from direct nest protection against agriculture machinery or using nest cages against predators to launching large scale agri-environmental schemes in agricultural landscape and creation of international agreements over the net of protected areas connecting continents along migratory routes of shorebirds (Isaksson *et al.*, 2007; Delany *et al.*, 2009; Colwell, 2010; O'Brien & Wilson, 2011; Laidlaw *et al.*, 2017). However, the effectiveness of some conservation measures is questionable (Klejn *et al.*, 2001) highlighting the need for the "evidence-based conservation" (Sutherland *et al.*, 2015). Therefore in **Chapter 4** (Zámečník *et al.*, 2018), we assess the effectiveness of direct nest protection against agriculture machinery from nest predation point of view. Conservation of shorebirds and their habitats is even more urgently important right now, when majority of shorebirds is declining globally (Munro, 2017; Studds *et al.*, 2017; BirdLife International, 2018). In **Chapters 5**, **12** and **13,** we discuss shorebird conservation from agri-environmental scheme or world-wide scale recommendation perspectives.

The role of predation in population dynamics

The whole population dynamics, the decline, stability or increasing trend of any species is given by its reproductive output and adult survival, in majority of populations, the immigration and emigration play an important role as well (e.g. Ricklefs, 1983; Cappuccino & Price, 1995). The reproductive output consists of the mean number of clutches laid per year, number of eggs per clutch, proportion of eggs hatching, proportion of chick fledging and the age of first breeding (Evans & Pienkowski, 1984; Colwell, 2010). Furthermore, survival can differ between sexes (Méndez *et al.*, 2018). Therefore, it is obvious that in such complex scenario, the predation is only one of possible mortality factors influencing the reproductive output (Bennett & Owens, 2002) and it is generally perceived that adult survival variation can affect population dynamics more that variability in reproductive output (e.g. Hitchcock & Gratto-Trevor, 1997; Sandercock, 2003; Piersma *et al.*, 2016). But since predation is the most important cause of breeding failures in shorebirds, possible high predation loses, lowering the reproductive output (Evans & Pienkowski, 1984; Colwell, 2010) – unless compensated by very high adult survival – could precipitate into population declines. Indeed, it has been shown that predation of nests and chicks can play an important role in population dynamics regionally or in particular years (Troy, 1996; Ganter & Boyd, 2000; Meltofte *et al.*, 2007; Roodbergen *et al.*, 2012), but global perspective has been lacking. Therefore in **Chapter 13**, we try to assess the relative importance of nest predation for decreases and increases in global population trends of shorebirds. Furthermore, our understanding to factors influencing population dynamics is important from conservation perspective (Colwell, 2010), therefore in **Chapter 12**, we perform comprehensive analysis trying to disentangle contributions of life-history or environmental traits and also known threats such as for example introduced predators to global population dynamics in shorebirds.

Outline of the thesis

Chapters in this thesis are structured into three sections. The first part focuses on the role of predation during reproduction of shorebirds inhabiting European agricultural landscape (**Chapters 2–5**). In the second part, the emphasis is given on interspecific relationships among breeding shorebirds or between shorebirds and other birds (**Chapters 6–10**). The third part of this dissertation (**Chapters 11–13**) explores a global perspective of predation and life-history strategies of shorebirds using comparative methods and data from all over the world (Fig. 2).

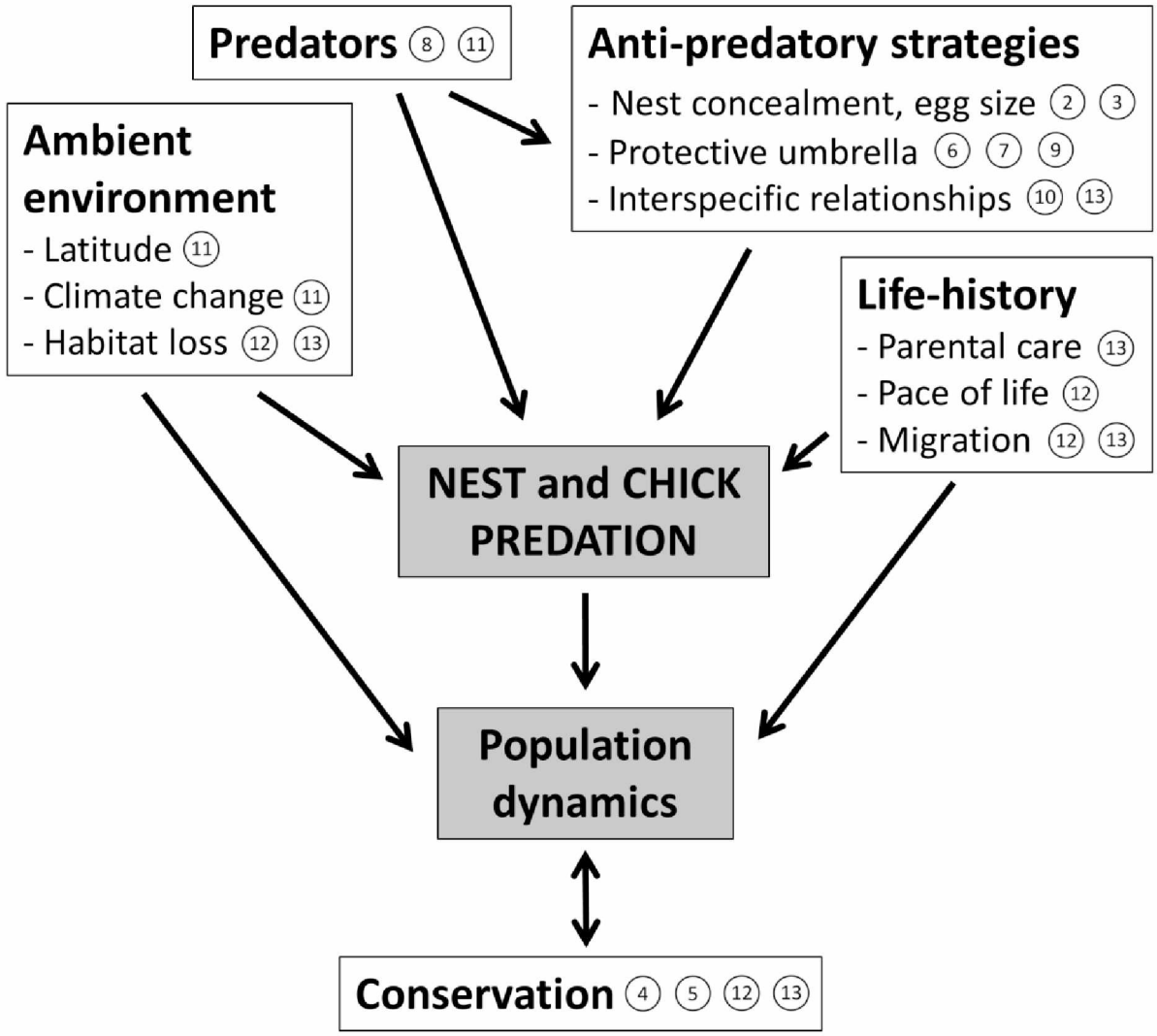

Figure 2. Outline of the thesis. Schematic representation of (hypothetical) relationships for factors affecting predation rates and population dynamics in shorebirds. Arrows indicate key relationships addressed in this thesis with relevant chapters given by the numerals.

Chapter 2 starts off with the investigation of behavioural plasticity in nest lining size. Variability in the nest lining is great in Northern Lapwing provoking a question about the possible trade-off between a thermoregulatory function of massive nest lining and its

conspicuousness for potential predators at the same time. There is no evidence for anti-predatory behaviour in the decision how large the nest lining to build. However, the thermoregulatory hypothesis is supported by the fact that lapwings are building larger nest lining next to water pools with cooler microclimate. The role of egg size variability for chick survival and predation risk in Northern Lapwing is discussed in **Chapter 3.** Heavier chicks from larger eggs are in better body condition, they more effectively search for food and more easily escape from predators, therefore it is important to understand factors influencing the egg size variability. Based on data from 15 lapwing populations, seasonality seems to be the best predictor of egg size variability, where eggs in first clutches are on average by 5–6% larger than eggs in replacement ones. Together with the fact that food is more available for chicks at the beginning of the breeding season, bigger eggs represent the double advantage of first breeding attempts from the population dynamics as well as conservation point of view. In **Chapter 4**, the applicability of a new direct nest protection measure against agriculture machinery is evaluated from nest predation perspective. Two thin 2 m long bamboo poles placed 10–15 m apart with the nest in the middle represent a finely tuned solution how to mark shorebirds nests. Such treatment is obvious for an informed farmer during the field management but it is not increasing the nest predation rate which is essential finding for wider effective application of this conservation measure. **Chapter 5** describes numbers, trends, distribution, breeding habitats, predation pressure, other threats and conservation measures for five meadow breeding shorebirds in the Czech Republic and Slovakia. All species have undergone decline similarly to other European countries, however, some of these declines are levelling off in last decades. New agri-environmental scheme on arable land, consisting of the ploughed field on traditional lapwing breeding grounds left without any management during the breeding season, seems to be working well – promoting not only breeding shorebirds but also other organisms, otherwise rare in conventionally managed arable land.

In **chapter 6**, Northern Lapwing nest scrape reuse by Little Ringed Plover is described for the first time together with the review of other 23 cases of interspecific nest scape reuse among shorebirds. This behaviour could be triggered in plovers by seeking for the protective umbrella in the breeding colony of lapwings, which are actively repelling potential avian predators from their breeding grounds. **Chapter 7** brings us to the pristine wetland habitat on the bank of Bajkal lake in Russia for closer investigation of inter-specific breeding associations of shorebirds and other water birds. Among tested anti-predator tactics, active nest defence is the most successful one in preventing nest depredation. Passive nest defenders benefit from breeding in close proximity of active defenders and by better nest concealment. **Chapter 8** goes a step further and tries to disentangle contributions of habitat, conspecific attraction and heterospecific protection "umbrella effect" in nest spatial distribution at the same locality. Results suggest the key importance of active nest defenders – their absence can dramatically impoverish whole breeding community regardless of the breeding habitat quality. **Chapter 9** investigates similar inter-specific interactions in associations of shorebirds breeding in natural steppe lakes near the Caspian Sea. Despite anti-predatory protective umbrella of terns in mix-species colonies, shorebirds as well as terns are experiencing extremely high nest predation rates and thus questioning the effectiveness of these anti-predatory tactics. However further monitoring in the region is needed for assessing the

temporal stability of reported nest predation patterns. **Chapter 10** concludes the second section of this thesis with a review of inter and intraspecific predation behaviour among shorebirds. These elegant creatures are not eating bivalves, worms or insect only, but they can purposefully predate on nests or chicks of other shorebird species. Mainly bigger shorebirds which are also aggressive nest defenders can occasionally eat eggs of other shorebirds, however, among turnstones, bird egg depredation is more common foraging strategy.

In **chapter 11**, nest predation patterns are viewed from large spatial and temporal perspectives with use of 38,191 nests from 237 populations in 111 shorebirds species from 149 localities at all continents, covering the time span of last 70 years. There are three main novel outputs from this study: 1) the first global evidence for the latitudinal gradient in offspring predation of wild populations with the highest historic predation rates in the tropics; 2) an extremely rapid increase in nest predation recorded in the North temperate region and especially in the Arctic recently; 3) a revealed link between climate change and nest predation rates, thus demonstrating a global-scale impact of climate change on trophic interactions between predators and prey. In **Chapter 12**, population dynamics, namely trends for 184 shorebird species are targeted together with environmental and life-history factors possibly affecting global population decline or increase in shorebirds. Declines are more likely found in species with shorter generation times and longer migration distances, indicating problems in Arctic breeding species similarly to chapter 11. On the other hand, global population increases are associated with island endemics suggesting a success of conservation actions in these species, often connected with an eradication of introduced predators. **Chapter 13** discuss the main outputs of this dissertation and outlines further avenues for future research.

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Northern Lapwing (*Vanellus vanellus*) nests in clover field and marshland, Czech Republic, 2016

Chapter 2

Great variability in the nest lining size: support for thermoregulation but not for anti-predatory adaptation hypothesis

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(manuscript)

Great variability in the nest lining size: support for thermoregulation but not for anti-predatory adaptation hypothesis

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Nest lining is a key component in nests of many bird species. Among ground-nesting birds with open nests, it usually consists of dry sticks and the stalks of plants which create a thermoregulatory insulating layer for the eggs. On the other hand, a massive nest lining can attract predators and increase nest mortality. However, factors influencing behaviour plasticity in birds facing the trade-off between nest lining thermoregulation and conspicuousness for predators have remained poorly understood. The Northern Lapwing *Vanellus vanellus*, biparentally incubating shorebird, performs a great variability in the size of nest lining and, at the same time, is subject to a high risk of nest predation. We analysed the variability of nest-lining size across time and space in 915 measurements of 601 real lapwing nests in South Bohemia, Czech Republic, during 2010–2015. We show that lapwing nests placed closer to small water pools with generally cooler microclimate had more massive nest lining. Nest lining size also reflected the nest lining material availability in the vicinity of the nest. On the other hand, there was no effect of nest position within the breeding colony and distance to the nearest tree as a possible perch for predators on nest lining size. Furthermore, nest lining size did not predict nest predation rate. Our findings infer that lapwings are adjusting their nests lining to local microclimate conditions more than they are solving the potential predation risk which is in concordance with the thermoregulation hypothesis of the nest size in birds.

Key-words: anti-predatory adaptation hypothesis, ground-nesting, microclimate, nest lining, nest predation, Northern Lapwing, shorebirds, thermoregulation hypothesis, waders

INTRODUCTION

Majority of bird species build open nest cups lined with dry plant material and/or soft feathers (Hansell & Deeming, 2002; Gill, 2007; Deeming & Reynolds, 2015). Principal function of nest lining is thermoregulation of the clutch (Reid *et al.*, 2002; Tulp *et al.*, 2012; Heenan, 2013), even though protection of eggs against mechanical damage as well as attracting sexual partners have been referred to play a role in some species (del Hoyo *et al.*, 1996; Hansell & Deeming, 2002; Deeming & Mainwaring, 2015). Incubation temperature and the amount of heat supplied at certain stages to embryo development may dramatically affect metabolic processes and contribute to the quality of hatchlings (Starck & Ricklefs, 1998). Moreover, massive nest lining can significantly reduce the energetic costs of incubating adults (Reid *et al.*, 2002; Tulp *et al.*, 2012).

On the other hand, a massive nest lining with the excellent thermoregulatory function may increase nest detectability for visually oriented predators (Mayer *et al.*, 2009; Mainwaring *et al.*, 2015). Indeed, some studies found bigger nests being more likely depredated in comparison with smaller ones (Grégoire *et al.*, 2003; Antonov, 2004; Biancucci & Martin, 2010). Therefore in deciding how to construct their open nest, breeding adults are facing a trade-off between providing a substantial lining to strengthen the thermoregulatory function of the nest or choosing a scanty lining to reduce the risk of nest predation (Ricklefs, 1983; Deeming & Reynolds, 2015).

Despite decades of intensive research on nest morphology (Deeming & Mainwaring, 2015; Mainwaring *et al.*, 2015; Martin *et al.*, 2017), the extent to which individual birds can use environmental cues to fine tune the morphology of their nest is still unclear (Healy *et al.*, 2015) and further research is needed on how nest size interact with nest location and parental behaviour (Mainwaring *et al.*, 2015). The aforementioned scenario presents an opportunity to investigate effects of external factors on the behavioural plasticity of individual breeding birds that may have consequences for nesting success, productivity and inevitably species population dynamics.

Nest lining is characteristic for the ground-nesting shorebird, Northern Lapwing (*Vanellus vanellus*), hereafter lapwing. This species breeds across Eurasian temperate zone with moderate climate where it builds open nests predominantly on bare grounds with sparse or absenting vegetation in agricultural landscape (Cramp & Simmons, 1983; Nethersole-Thompson & Nethersole-Thompson, 1986; Shrubb, 2007) and is subject to a high risk of nest predation (e.g. Cramp & Simmons, 1983; Šálek & Šmilauer, 2002; MacDonald & Bolton, 2008; Roodbergen *et al.*, 2012). Lapwing nest lining size is highly variable from sparse to very massive nest lining in this species (Cramp & Simmons, 1983; Shrubb, 2007) and consists of plant material, predominantly dry stalks of cereals and grasses. The building of each nest continues with progressive filling the excavated scrape with plant material particularly during pre-laying and laying periods by both male and female (Cramp & Simmons, 1983; Nethersole-Thompson & Nethersole-Thompson, 1986; Shrubb, 2007) and may thus function as a part of display ritual (Cramp & Simmons, 1983). However, environmental factors affecting nest lining size remain poorly understood.

The aim of this study is to investigate factors influencing the variability in nest lining size and test whether there is an evidence for anti-predatory adaptation or thermoregulation hypothesis. Specifically, with use of Northern Lapwing as model species, we are asking: (i) What is the variability of nest lining size? (ii) Which factors (nesting habitat, nest site moisture, nest lining material availability, incubation start date, position within breeding colony and distance to the nearest perch for potential predators) predict the nest lining size? (iii) Is there any relationship between nest lining size and nest predation rate?

MATERIALS AND METHODS

Study population and data collection

We searched for the Northern Lapwing nests in České Budějovice basin in the centre of South Bohemia (49.0° N, 14.4° E) in the Czech Republic during 2010–2015. The study area consists of circa 60 km² of agricultural landscape with prevailing arable land in altitude 380–420 m, for more details, see (Šálek & Šmilauer, 2002; Zámečník *et al.*, 2018). We searched for nests at the places with the breeding presence of lapwings using binoculars and scopes, or direct physical investigation of dense breeding colonies during the breeding season, regularly end of March to April or May each year.

We recorded nest GPS coordinates and we assigned each nest into the one out of three categories according to habitat structure (table 1). We determined the day of incubation start for each nest with use of floatation method (van Paassen *et al.*, 1984) or according to known egg-laying sequence (incubation start = a day when the third egg was laid). During every visit, we took a digital picture of the nest from 1 m directly above the nest with 35mm optical distance to capture the nest and close surrounding up to 1 m from the nest to be able to evaluate the size of nest lining. During 2014–2015 we took also an additional picture from 2m directly above the nest with 35mm optical distance to capture wider surrounding up to 2m from the nest for nest lining material availability description purpose. We followed the fate of each nest and determined nest as successful (hatched or survived particular period), predated or failed for other reason. Every nest where at least one chick hatched was regarded as successful. A hatched nest was recognised according to tiny egg-shell fragments remaining in the nest scrape from the hatching process (Green *et al.*, 1987). Clutches with unfertile eggs with present parents which had not been depredated over expected egg-laying and incubation period were regarded as successful ones for the purpose of predation analyses. Only complete nest depredations were included in the predated nests category (partial egg loss were omitted). Predated nests were recognised according to missing eggs before estimated hatching with no marks suggesting another cause of failure or according to remnants of depredated eggs in the nest or close vicinity.

Data processing

Three authors of this study independently scored nest lining size from digital nest images according to prepared scale into one of eight categories: 0.5–4 (see an example in Fig. 1). The arithmetic mean value vas further used for each nest at each nest visit in subsequent analyses. Repeatability among evaluators estimated by function "rpt" (Nakagawa & Schielzeth, 2010; Gaussian model) was 72%. Lining thickness at the bottom of active nests strongly correlated with the lining size scored from photographs (Pearson´s $r = 0.78$, $P < 0.001$, $n = 18$ active nests in 2014), therefore the nest size scored from photographs were used in all analyses as reliable predictor of the nest lining magnitude in the bottom as well as at the sides of the nest scrape. Furthermore, V.K. determined the nest site moisture up to 1m from the nest with use of digital nest images into three categories 0 – dry nest site; 1 – moist nest site; 2 – open water (pool) present up to 1 m from the nest. Because the site moisture category was clearly obvious

from the picture, only one person was involved in this process. Nest site moisture constitutes a predictor for the thermoregulatory hypothesis because wetter places tend to have cooler microclimate (e.g. Reid *et al.*, 2002; Rogers *et al.*, 2006; Yang *et al.*, 2013).

Three independent evaluators (see acknowledgement) without knowledge of nest lining size and the purpose of the assessment scored the nest lining material availability from digital nest images according to prepared scale into one of three categories 0–2 (Fig. 2). The arithmetic mean value vas further used for each nest at each visit in subsequent analyses. Repeatability estimated from by function "rpt" (Nakagawa & Schielzeth, 2010) was 61%. Every nesting habitat was assigned into one of three categories according to habitat structure (table 1).

Because nest placement can affect the nest predation probability in our study population (Šálek & Šmilauer, 2002) and visually oriented predators may play a role (Šálek & Zámečník, 2014) and thus lapwings could adjust nest lining size to nest predation risk, we assigned according to known nest GPS coordinates each nest into three following categories of the nest position in the breeding colony: 1 – solitary nest placed outside of any breeding colony (at least 200 m from the nearest lapwing nest); 2 – edge nest creating a polygon of all nests present in a breeding colony with less than 200 m distance to the nearest lapwing nest; 3 – interior nest placed within the polygon of edge nests in a particular breeding colony with less than 200 m distance to the nearest lapwing nest. Furthermore, with use of measuring ground distance tool in Google Earth (ver. 7.1), we measured in meters the distance of each nest to the nearest potential perch for avian predators (tree or any structure higher than 5 m).

From the given mean day ambient temperatures in České Budějovice (Czech Hydrometeorological Institute in litt.) at the edge of study area (altitude of 395 m), we computed mean ambient temperature value in °C from five days prior the day of incubation start (excluded) to estimate the general harshness of environmental condition in our study area just before and during the egg laying when lapwings are building the nest lining (Cramp & Simmons, 1983).

We computed daily nest predation rates according to Mayfield defined as the number of predated nests divided by the exposure of all nests in days (Mayfield, 1961, 1975). The procedure of computing the exposure for daily nest predation is defined as follows. The exposure for hatched nests is from a day of finding until known or predicted hatching (e.g. 11 April and 28 April means 28-11 = 17 days of exposure). The exposure for depredated nests is from day of finding until midpoint assumption between last positive and first negative visits of the particular nest, the exposure for failed nests due to any other reason than predation (e.g. agriculture machinery, nest abandonment) or for nest with an unidentified fate is from day of finding until the last positive visits (not midpoint assumption between last positive and first negative visits of the nest).

Statistical analyses

Statistical analyses were performed with R, ver. 3.3.3 (R Development Core Team, 2017). We used linear mixed-effect models (Crawley, 2013) with control for all remaining predictors in the model and with a random effect of the year. We used the general linear model for the

relationship between daily predation rate and nest lining size. Linear mixed-effects models were fitted with the 'lme4' package (Bates & Maechler, 2012). Residuals from tests were checked for normality in a quantile-quantile plot (Crawley, 2013). All tests were two-tailed.

RESULTS

Nest lining size variability

Nest lining in the given population of Northern Lapwing is highly variable, ranging from 0.25–4 of mean score, mean = 1.91, median = 1.83, (Fig. 3). There is no meaningful change of nest lining size during the incubation (Fig. 3) and incubation stage in reasonable range of 1–25 days do not influence nest lining size (LME: df = 1;555, F = 2.51, P = 0.110, random factor: year, 561 measurements of 561 nests).

Factors affecting nest lining size

Nest lining size was influenced by nest site moisture and nest lining material availability. Breeding habitat was no longer significant after control for nest lining material availability. Ambient temperature, incubation start date, position in the colony and distance to the nearest perch for potential predators were non-significant predictors of nest lining size (table 2). Bigger nest lining was found in wetter nest sites (Fig. 4) and at sites with higher nest lining material availability (Fig. 5).

Nest predation rate

Nest lining size did not predict daily nest predation rate (GLM: cbind (fate of the nets, exposition in days) ~ nest lining size, family = binomial, z = 0.60, P = 0.552, n = 590 nests during 2010–2015).

DISCUSSION

We have found that nest lining size in Northern lapwing is influenced by nest site wetness and nest lining material availability but not affected by ambient temperature, incubation start date, nest position within the breeding colony or nest distance to the nearest perch for potential predators. The effect of breeding habitat is significant only without control for nest lining availability. Furthermore, we have shown that the nest lining size does not predict the daily nest predation.

Bigger nest lining is found at wetter nest sites, especially when open water pool is closer that one meter from the nest. Our finding is in line with general assumption that thermoregulatory function of the nest is important (Deeming & Reynolds, 2015), especially in ground-nesting species breeding in extreme climate of high Arctic (Tulp *et al.*, 2012) or alpine environment (Camfield & Martin, 2009). Thus Arctic shorebirds prefer to breed on slopes with milder microclimate (Meltofte *et al.*, 2007) and use specific lining material to

reduce heat loss from nests (Reid *et al.*, 2002). Detailed study on nest design of the Pectoral Sandpiper (*Calidris melanotos*) from areas with permafrost confirmed that the birds reduce the rate of heat loss from the nests using the lining of nest scrapes and that deeper nest cups are more effective in heat retention (Reid, Cresswell et al. 2002). We may assume that just a specific layer of dry stalks containing sufficiently large air cells has effective insulating function against environmental harshness (Deeming & Mainwaring, 2015) and could play an important role also for shorebird species breeding in temperate agricultural landscape, particularly in wet places with cooler microclimate (e.g. Reid *et al.*, 2002; Rogers *et al.*, 2006; Yang *et al.*, 2013). No effect of ambient temperature on nest lining size can seem to be contradicting the thermoregulatory hypothesis. However, the slight trend of bigger nest lining sizes during lower temperatures, though non-significant, is rather suggesting that from the egg insulation perspective, the local microclimate (nest site wetness) plays a more important role than average ambient temperatures over the whole study area.

Nest lining size is bigger at places with higher nest lining material availability. This finding is not surprising given the fact that that nest lining behaviour performed by both parents can be a part of display ritual (Cramp & Simmons, 1983; Nethersole-Thompson & Nethersole-Thompson, 1986; Shrubb, 2007). This ritual can be partially done also without plant material (Cramp & Simmons, 1983), therefore ritual intensity does not have to be more intense at sites with more nest lining availability. Thus lapwings are simply using plant material more when it is available in the nest surrounding, which is the case, especially in more vegetated nesting habitat. Similarly, Piping Plovers (*Charadrius melodus*) used more shell fragments in their nest lining when the nest was located on shelly, rocky, or coarse-sanded beaches (Greenwald, 2009). Generally, birds quite often follow the nest material availability (quality and quantity) during nest building (Deeming & Mainwaring, 2015).

While bigger nests are more obvious for potential predators (Grégoire *et al.*, 2003; Antonov, 2004; Biancucci & Martin, 2010) and visually oriented predators play a role in our lapwing study population (Šálek & Zámečník, 2014), there is no significant effect of nest position within the breeding colony or nest distance to the nearest perch for potential predators on the nest lining size and no effect of the nest lining on daily nest predation rate. These findings can have several not mutually exclusive explanations: i) breeding Northern Lapwings, well known aggressive nest defenders (Elliot 1985b, Liker & Székely 1999, Kis *et al.* 2000) can effectively repel potential avian predators from breeding grounds, and therefore they are not forced to make nest lining smaller under higher risk or depredation (nest placement close to perches for predators outside of breeding colony); ii) visually oriented predators play a minor role in our study population where predominantly mammals were recognized as nest predators (Kubelka, 2015); iii) nest lining size per se could not be the important clue for visually oriented predators during nest search, but rather other stimuli, e.g. visibility of incubating parent (Šálek & Zámečník, 2014) could play more important role for nest predation rate.

The presented study provides several insights into the long-standing debate on the trade-off between nest size thermoregulatory function and conspicuousness for predators at the same time (Ricklefs, 1983; Deeming & Reynolds, 2015). First, while using large sample

sizes over six years, it shows that lapwings are adjusting their nest lining size to the local microclimate, building larger nest linings in wetter nest locations, thus providing support for thermoregulatory functions of the nest lining. Second, also nest lining material availability is the significant predictor of nest lining size and effect of both predictors can be additive. Third, nest lining size is not adjusted to presumed nest predation risk and it does not predict nest predation rate, suggesting that lapwings in South Bohemia are not forced to reduce nest lining size as the anti-predatory adaptation.

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FIGURES AND TABLES

Figure 1. The scale of Northern Lapwing (*Vanellus vanellus*) lining size variability. South Bohemia, Czech Republic. **(a)** Nest with nest lining size scored as 1 – sparse nest lining; **(b)** Nest with nest lining size scored as 2 – obvious nest lining but not meaningfully extend the nest scrape rim; **(c)** Nest with nest lining size scored as 3 – distinct nest lining well extended beyond the nest scrape rim; **(d)** Nest with nest lining size scored as 4 – massive nest lining. Photographs credits: a–c Vojtěch Kubelka, d Vladimír Štorek.

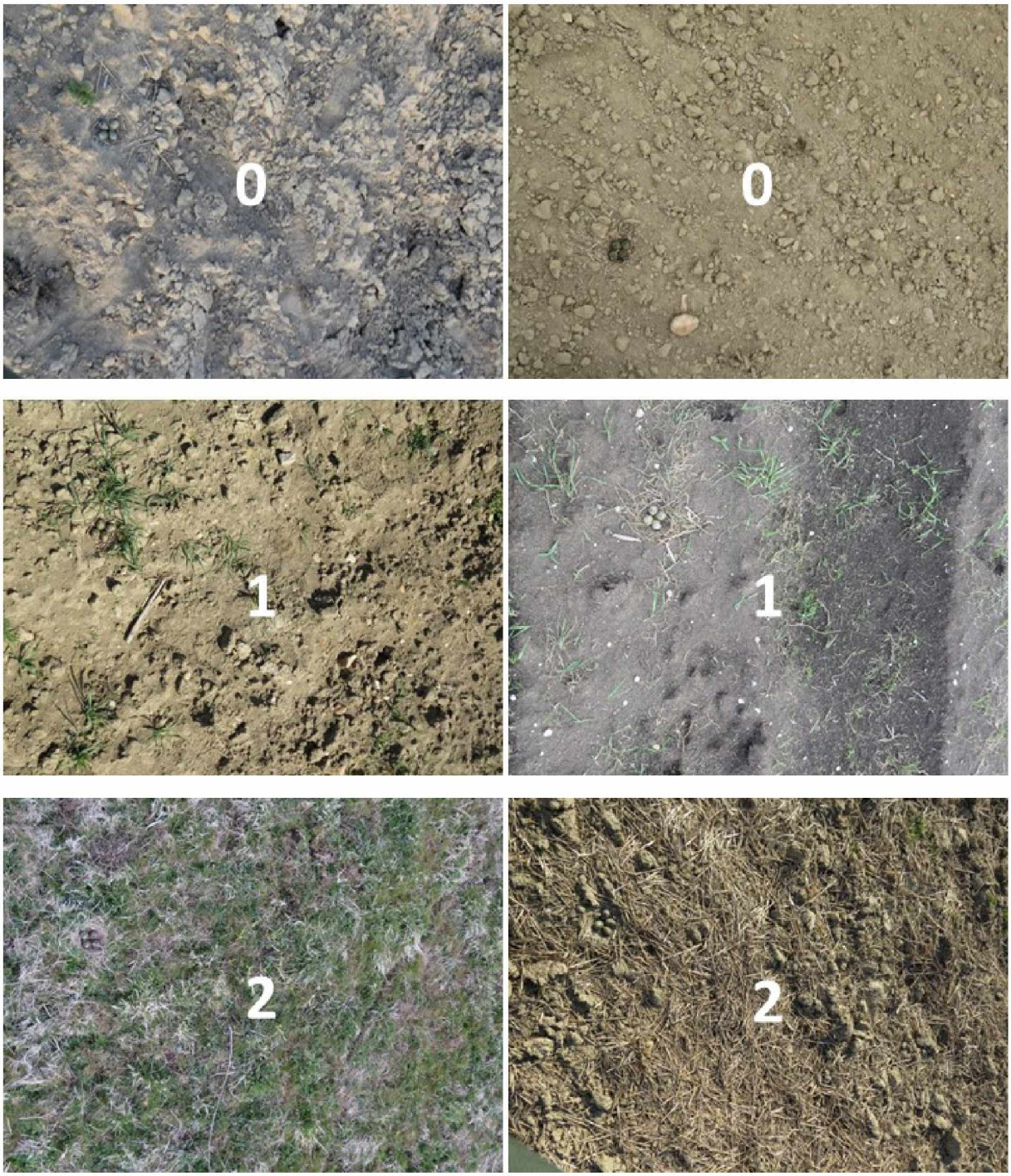

Figure 2. The scale for nest lining material availability in the vicinity of the nest. (0) nothing or a little; (1) sort of; (2) plenty. Photographs credit: Vojtěch Kubelka.

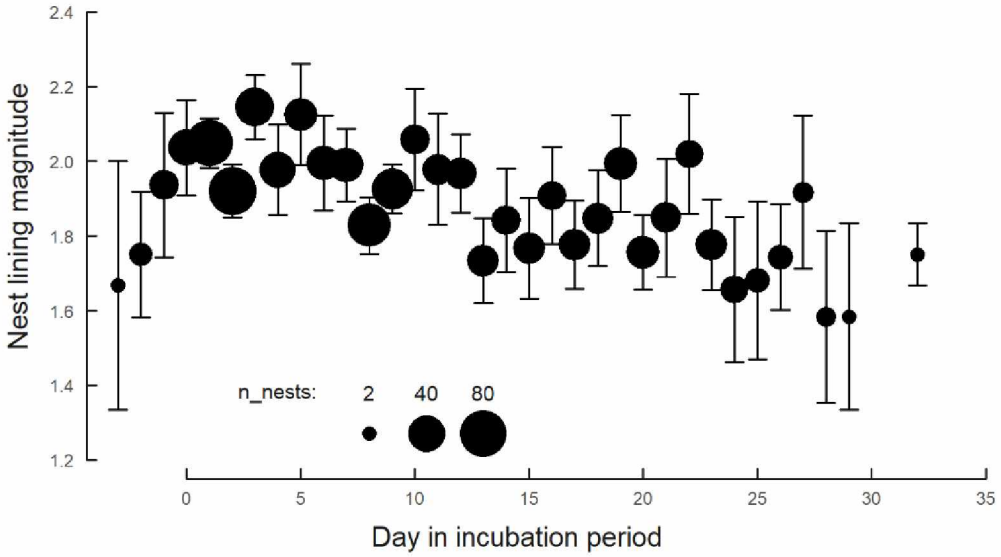

Figure 3. Nest lining size variability during incubation. Size of the dots reflects the sample size, error bars = SE, n = 915 measurements of 601 lapwing nests from 2010–2015 in South Bohemia, Czech Republic. See Methods for scoring procedure and Fig. 1 for nest lining size category examples.

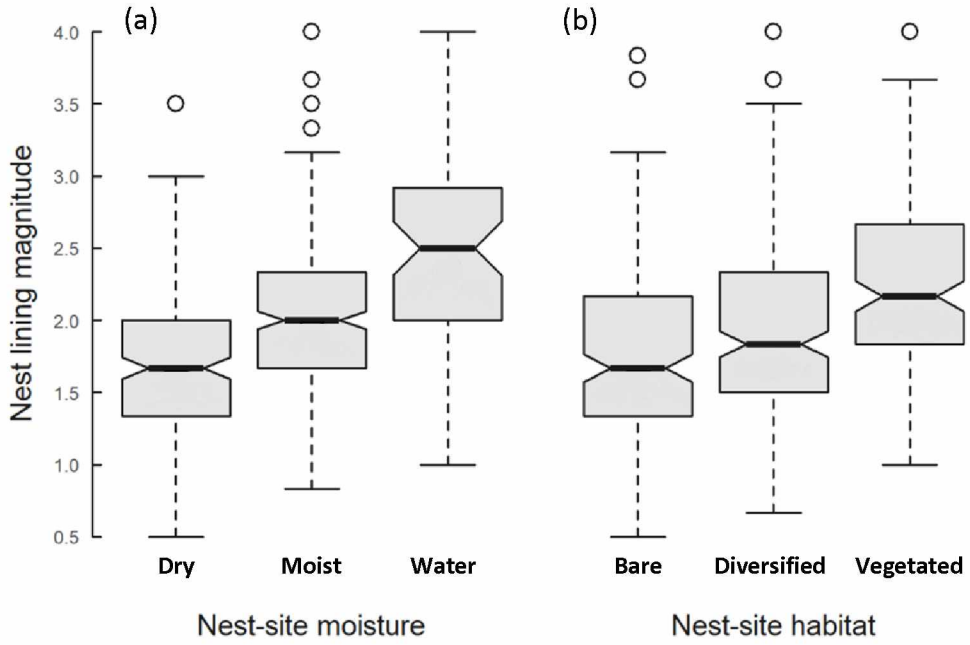

Figure 4. Lining nest size relationship with nest site moisture **(a)** and breeding habitat **(b)**. Box-plots represent two decades before and six decades after the median of incubation start each year. Medians, quartiles, 1.5 inter-quartile range and outliers are presented, n size = 557 nests during 1988–2018 in South Bohemia, Czech Republic, particular sample sizes in number of nests are follows: Dry = 201, Moist = 296, Water = 60, Bare = 186, Diversified = 212, Vegetated = 159, for more details see table 1.

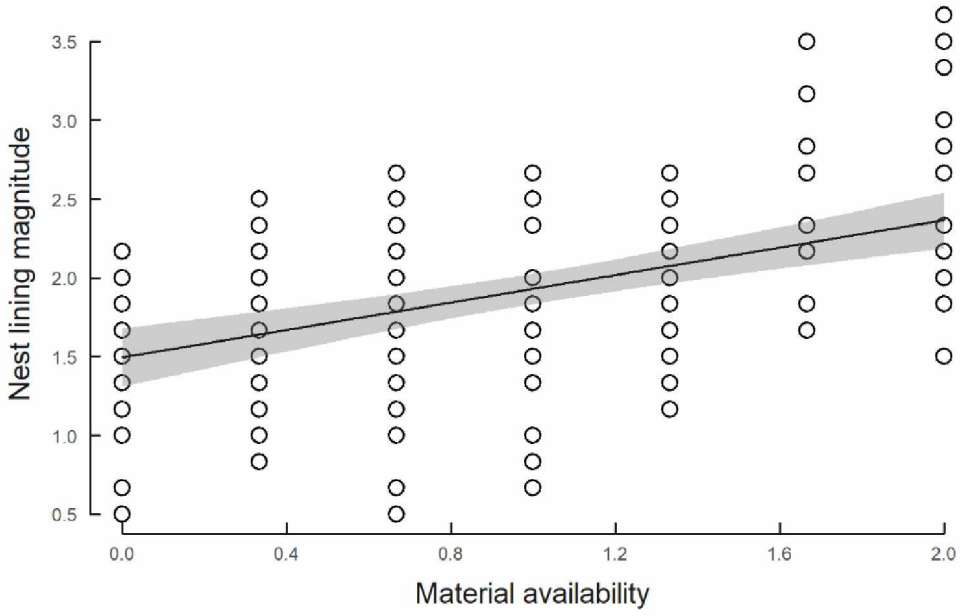

Figure 5. Effect of nest lining material availability on nest lining size in 191 nests from 2014 and 2015. Line with shaded area indicate model prediction with 95% credible intervals based on the joint posterior distribution of 5 000 simulated values based on model outputs (table 2) and generated by the 'sim' function in R (Gelman *et al.*, 2016).

Table 1. Habitat categories distinguished in the study.

Category	Description of physiognomy	Crops merged
1	Structurally uniform bare field without or with little vegetation	Freshly harrowed or sown spring cereal, maize, bean
2	Structurally diversified plot without or with mosaic vegetation	Ploughed field, sparsely overgrown fallow, stubble
3	Continuously vegetated areas	Winter cereal, grassland, oilseed, clover

Table 2. Effect of nest site moisture, nest lining material availability, breeding habitat, ambient temperature, incubation start date, position in the colony and distance to the nearest perch for potential predators on nest lining size in South Bohemia, Czech Republic. Linear mixed effect model with the random effect of year, all predictors were controlled for the effect of remaining ones – type III analysis. All significant predictors are kept in subsequent models. (a) n = 557 nests during 2010–2015. (b) n = 418 nests during 2011–2015 with measured position in the colony and distance to the perch. (c) n = 191 nests during 2014–2015 with measured nest lining material availability. No predictors were inter-correlated (table 3). See Methods for more details and table 1 for habitat descriptions.

(a) whole dataset 557 nests

Predictor	***df***	F	***P***
Nest site moisture	2 ; 320	71.97	<0.001
Breeding habitat	2 ; 300	18.64	<0.001
Ambient temperature	1 ; 442	1.55	0.210
Incubation start date	1 ; 101	0.71	0.400

(b) reduced dataset 418 nests

Predictor	***df***	F	***P***
Nest site moisture	2 ; 257	25.67	<0.001
Breeding habitat	2 ; 400	16.73	<0.001
Position in the colony	2 ; 408	1.55	0.360
Distance to the perch	1 ; 409	0.71	0.470

(c) reduced dataset 191 nests

Predictor	***df***	F	***P***
Nest lining material availability	1 ; 161	25.16	<0.001
Nest site moisture	2 ; 184	3.84	0.020
Breeding habitat	2 ; 115	0.24	0.780

Table 3. Correlation matrix of all potential predictors of nest lining size. N = 191 nests from 2014–2015, South Bohemia, Czech Republic.

	STI	offer	temp	moist	posit	perch	habit
Incubation start date (STI)	1						
Nest lining material availability (offer)	-0.24	1					
Ambient temperature (temp)	0.54	-0.16	1				
Nest site moisture (moist)	0.05	0.18	0.07	1			
Position in the colony (posit)	0.01	-0.13	0.05	0.00	1		
Distance to the perch (perch)	-0.15	0.38	-0.10	0.04	0.04	1	
Breeding habitat (habit)	-0.55	0.64	-0.33	0.09	-11	0.31	1

Clutch of Northern Lapwing (*Vanellus vanellus*) hatching South Bohemian lanscape, Czech Republic, 2012

Chapter 3

Seasonality better than nesting habitat predicts egg size in precocial shorebird

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(submitted manuscript)

Seasonality better than nesting habitat predicts egg size in precocial shorebird

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Egg size represents a fundamental predictor of chick mass and body condition. Bigger egg size significantly rises chances for offspring survival, especially in precocial species, where chicks must forage themselves and cope with environmental harshnesses such as bad weather or predators. The advantage of the big egg can be apparent beyond the fledging stage. Therefore our understanding of factors influencing the egg size is crucial from breeding ecology as well as conservation perspectives. However, simultaneous addressing of more factors and quantifying their influence on the egg size with use of large sample size is rare. Here, we test the effect of seasonality, clutch size and nesting habitat on the egg size in ground-nesting shorebird, the Northern Lapwing (*Vanellus vanellus*), on sample of 4,384 eggs from 1,125 clutches in South Bohemia, Czech Republic, during period 1988–2018. We report significant decline of the egg size over the breeding season, on average bigger eggs in larger clutches with significant difference between 2-eggs and 4-eggs clutches and no direct effect of nesting habitat. From the review of the same predictors over 15 Northern Lapwing populations though Europe is apparent that replacement or late clutches have on average by 3–7% smaller eggs than first or early clutches. Nesting habitat affects the egg size only rarely in less heterogeneous landscapes. In general, arable land supports slightly bigger eggs in comparison to pastures or heathland. There are no significant egg size differences between 3-eggs and 4-eggs clutches. Taken together, the better performance of chicks hatched from bigger eggs early in the breeding season in combination with higher food abundance available for chicks by that time represent a clear message for conservationists and policymakers – early breeding attempts may play a pivotal role in shaping shorebird breeding productivity and the whole population dynamics.

Key words: clutch size, chick survival, egg size, nesting habitat, Northern Lapwing, precocial offspring, predation, seasonality, *Vanellus vanellus*, wader

Introduction

Egg size in birds is not only a measure of parent's investment into offspring, but also represents an important predictor of chick growth and survival (Williams, 1994; Christians, 2002; Krist, 2011). In general, egg size is more important for precocial birds, where chicks soon after hatching must forage themselves and they are more exposed to harsh climatic conditions or predators in comparison with altricial nestlings in the nest (Starck & Ricklefs,

1998). Precocial birds influence survival of their chicks by higher investment into eggs, which are on average proportionally larger and more energy-rich when compared to eggs of altricial bird species (Starck & Ricklefs, 1998; Deeming, 2002) and shorebirds belong to the bird clades with proportionally largest eggs (Rahn *et al.*, 1975).

The positive relationship between egg size and chick size has been found in many bird species (Martin, 1987; Christians, 2002; Krist, 2011) as well as several shorebirds (Byrkjedal & Kålås, 1985; Galbraith, 1988b; Grant, 1991; Thompson & Hale, 1991; Hegyi, 1996; Blomqvist *et al.*, 1997; Hegyi & Sasvari, 1998; Dittmann & Hötker, 2001; Sheldon, 2002; Larsen *et al.*, 2003). The bigger chicks are in better body condition, they are capable of longer self-thermoregulation, they more effectively search for prey and more easily escape from predators. This advantage of hatching from the bigger egg can positively influence chick survival until fledging (Davis, 1975; Galbraith, 1988b; Bolton, 1991; Grant, 1991; Sheldon, 2002; Eglington *et al.*, 2010; Krist, 2011).

Higher variability in egg size is documented among clutches than within a clutch (Nol *et al.*, 1984; Redmond, 1986; Thompson & Hale, 1991; Blomqvist & Johansson, 1995; Dittmann & Hötker, 2001; Parish *et al.*, 2001) and it seems to be a characteristic feature of a particular female, because eggs in consecutive clutches of the same female are more similar in size than eggs from different females (Christians, 2002). Nevertheless, older, more experienced and heavier females lay bigger eggs than younger and lighter individuals of the same species (Nol *et al.*, 1984; Thompson & Hale, 1991; Parish *et al.*, 2001; Christians, 2002). Intrinsic factors of particular females such a protein storage or ovary size play probably an important role as well (Christians, 2002). Despite generally assumed pivotal role of female intrinsic characteristics (Christians, 2002), environmental factors, e.g. food availability during the egg formation period, can have not negligible influence on egg size (Lank *et al.*, 1985; Perrins, 1996; Nol *et al.*, 1997).

The Northern Lapwing (*Vanellus vanellus*), a precocial shorebird, similarly to most of Holarctic shorebirds (Lack, 1947; Arnold, 1999), lays predominantly invariant clutch size of four eggs (Klomp, 1970) and aggregates energetic reserves for egg production particularly after arrival to breeding grounds (Galbraith, 1989; Blomqvist & Johansson, 1995; Shrubb, 2007) and thus represents a suitable model species for investigation of environmental or physiological factors affecting the egg size (Galbraith, 1988b).

Our aim is to assess and quantify the role of factors influencing the egg size in Northern Lapwing with implications for conservation practice and we are asking particularly: (i) Does seasonality, nesting habitat or clutch size influence the egg size? (ii) Is chick size after hatching predicted by the egg size? (iii) What is the effect size of seasonality, nesting habitat and clutch size in Northern Lapwing from a comparative perspective and what are possible consequences for chick performance?

METHODS

Study area and field methods

We searched for the Northern Lapwing (hereafter referred as lapwing) nests near České Budějovice, the Czech Republic, during 17 breeding seasons between 1988 and 2018. The study area (centre: 49.0° N, 14.4° E) consists of approximately 60 km² of agricultural landscape with prevailing arable land in altitude of 380–420 m, for more details see (Šálek & Šmilauer, 2002; Zámečník *et al.*, 2018). Lapwings breed in the whole area in small aggregations (rarely > 15 pairs) or less commonly as individual pairs. We searched for nests using binoculars and scopes, or by direct physical investigation of denser breeding colonies during the breeding season. The peak of the start of incubation was regularly during two first weeks in April with the overall median on 7 April, the earliest clutch incubation started on 19 March in 2017 and the latest on 15 June in 2013.

We recorded nest positions and assigned nesting habitat into one of six categories (Table 1). We determined the first day of incubation for each nest using flotation method (van Paassen *et al.*, 1984) or according to known egg-laying sequence, incubation start = a day when the third egg was laid (Shrubb, 2007), for two egg clutches the date of second egg laying was used. We took eggs measurements (length, width) to the nearest 0.05 mm using a vernier calliper. Due to possible egg size differences according to laying sequence in one clutch (Lislevand *et al.*, 2005), only complete clutches were included. The final dataset contained 1,125 clutches with all eggs measured, known nesting habitat and defined first day of incubation.

Data processing

From egg measurements, we computed egg volume for each egg according to Galbraith's (1988) formula: $V = 0.457*L*W^2$, where V = egg volume, L = length of the egg in mm, W = width of the egg in mm. Then we converted the values to cm³ and calculated the mean egg volume for each clutch as the targeted response variable. We coded the first day of incubation for each clutch as a number of days since the start of the calendar year regardless the 29 February in leap years for easier comparability of data, thus value 91 = always 1 April and 152 = 1 June etc. Because warmer winters and wetter spring can accelerate the start of lapwing breeding season (Both *et al.*, 2005; Musters *et al.*, 2010) and the timing of breeding season was unique every year in our study population, we also computed standardized first days of incubation expressed as a number of days prior or after median of the first day of incubation for each year separately. There was no temporal trend in egg size variation for 1,125 clutches over 17 breeding seasons during 1988–2018 (LM: Estimate = -0.009 $F_{1,1123}$= 1.12, P = 0.282) which is important when addressing questions of this study.

Comparative perspective

We searched for suitable publications using keywords ("Northern Lapwing" or „*Vanellus vanellus*") in electronic databases: Web of Science, Searchable Ornithological Research

Archive and Google Scholar or via reference works (Cramp & Simmons, 1983; Shrubb, 2007; del Hoyo *et al.*, 2018) and references in relevant publications. We found 13 publications which held the information on egg size and at least one predictor used in this study, altogether with our two data sets accounting for 15 lapwing populations in the review.

Because of possible geographical variation in egg size of shorebirds generally (Väisänen, 1977) or lapwing particularly (Chylarecki *et al.*, 1997) and due to the fact of different egg volume computations or usage of egg mass instead of egg volume in some studies, for better comparison among populations, we expressed the effect size of each predictor as relative percentage difference between mean values of the tested categories and the overall mean egg size in particular dataset. Seasonality was reported in two ways: (i) comparison between first and replacement clutches known according to individually recognized birds; (ii) comparison between early and late clutches in the regression of the egg size according to first day of incubation over the breeding season of two months in total. In the case that the season was a little bit longer (Sheldon, 2002; this study), the effect size was adjusted for two months period only. Note that in two studies (Sheldon, 2002; Sharpe, 2006), the date was not standardized according to the median of first day of incubation each year, and therefore the seasonal change in egg size could be less apparent than in the case of standardization.

When reporting nesting habitat impact on the egg size, only Galbraith, (1988c) had proportionally balanced distribution of first and replacement clutches between two tested prevalent habitat categories and Murton & Westwood, (1974) had similar sample sizes between habitats for different months during the breeding season. Other studies did not account for the possible different proportion of first and replacement clutches between two tested habitats and one study (Cherkaoui & Hanane, 2011) even acknowledges the possible impact of this disbalance on the egg size. No study accounted for a possible influence of clutch size change over the breeding season (Shrubb, 2007), therefore it is necessary to interpret with caution the significance of reported values and the effect size comparison among studies for factors clutch size and nesting habitat.

We treated results only if more than 10 clutches were available per category, otherwise, we assigned the relationship as NA = no data available. In the case of Klabník (1984), we computed egg volumes from presented mean egg measurements according to the given formula (Galbraith, 1988b) and then computed differences from egg volumes. For the predictor effect size computation, in four studies (Murton & Westwood, 1974; Galbraith, 1988b; Baines, 1990; Blomqvist & Johansson, 1995) we computed mean egg volumes for each category from given subset values (divided e.g. by year or habitat) with usage of weighted mean according to sample size (number of clutches) in each subset. We used these values for the predictor effect size assessment by computing percentage difference between the mean values of tested categories from the overall mean egg size in the particular dataset of given lapwing population. Total values of the particular predictor effect size were computed as the mean weighted by sample size (number of clutches) across all studies reporting the relationship and its quantification.

Statistical analyses

All statistical analyses were performed with R ver. 3.3.3 (R-Core-Team, 2017). We performed general linear models using 'lm' function or general linear mixed-effects models fitted with the 'lmer' function from 'lme4' package (Bates & Maechler, 2012) with a year as a random intercept. Individual categories of nest habitat and clutch size were compared by post-hoc multiple comparisons of means (Tukey contrasts) in 'multcomp' package (Hothorn *et al.*, 2017). Residuals from all tests were checked for normality in quantile-quantile plot (Crawley, 2013). All statistical tests were two-tailed.

RESULTS

Effect of seasonality, clutch size and nesting habitat on egg size

The mean egg volume in the clutch varied from 19 to 28 cm^3, mean = 23.40 cm^3 ± 1.38 (SD), median = 23.44 cm^3, and declined significantly over the breeding season according to the first day of incubation for individual clutches (Figure 1, table 2). Also clutch size significantly predicted the mean egg size (table 2). Mean egg volume in 2-eggs clutches was by 4.1% smaller than in 4-eggs clutches (Tukey contrasts; z-value = 2.77; P = 0.005), other clutch sizes did not differ significantly, however egg size tended to increase with clutch size (Figure 2). There was no effect of nesting habitat after control for seasonality and clutch size (table 2). Nesting habitat was significant only when treated alone (LME; χ^2 = 58.51; df = 8, 5; P < 0.001, random factor: year), with on average smaller eggs in spring crops (table 3), in comparison with ploughed fields, meadows and winter crops (Tukey contrasts; all three P values < 0.001). In the comparison of three main habitats with similar mean first day of incubation (ploughed field, meadow and winter crop), the habitat category did not influence the mean egg volume in the clutch (LME; χ^2 = 3.50; df = 5 , 2; P = 0.174, random factor: year, n = 676 clutches).

Egg size and chick size

The mean chick mass in the clutch after hatching was significantly predicted by mean egg volume in the clutch (LM: Estimate = 0.701, $F_{1,44}$ = 99.32, P < 0.001) with heavier chicks hatching from bigger eggs (Figure 3).

Comparison among locations

The effect of seasonality (first clutches vs. replacement ones or regression of the egg size over the breeding season of two months) proved to be the significant predictor of the egg size in seven out of 11 cases (table 4). All 10 reported relationships were negative, generally clutches laid later in the season consisted of smaller eggs than clutches from the first part of the breeding season. The effect size indicated on average 5.6% (0.1–11.8%, n = 10 studies, 2,389 clutches) decline of the egg size through the breeding season. When first and replacement clutches were treated separately, the average decline was 2.9% (0.1–11.8%, n = 5 studies, 612

clutches), for the regression over the breeding season (two months) the mean effect was 6.5% (5.9–7.3%, n = 5 studies, 1,777 clutches). The influence of nesting habitat (the contrast between two most prevalent habitat categories) was significant in 4 out of 10 cases. On three occasions, eggs were found bigger in arable land compared to coastal pastures, rough grazed pastureland or heathland. In one case, eggs were bigger on wet meadows in comparison to saline grasslands. However, only in two of these studies partially accounted for the effect of possible disbalance of first and replacement clutches between compared habitat categories (see Methods), therefore it is important to interpret these results with caution. The effect size was on average 1.1% (0.2–6.0%, n = 7 studies, 2,190 clutches) between habitat categories (table 4). There were no significant differences in egg size between 3-eggs and 4-eggs clutch sizes in all seven studies. The effect size was on average 0.9% (-0.8–1.1%, n = 5 studies, 1,608 clutches) from the mean egg size (table 4).

DISCUSSION

We have reviewed the relative importance of three factors (seasonality, nest habitat and clutch size) influencing the egg size variability in Northern Lapwing in Europe, including for the first time performed predictor effect size assessment from the comparative perspective.

Seasonality

Seasonality has the most important effect on the egg size variability in lapwings where first clutches at the beginning of breeding season contain on average by of 5.6% larger eggs in comparison with late and probably replacement clutches. Finding of decline over breeding season is not surprising, because the fact that replacement clutches are generally smaller than the first ones have been reported repeatedly for lapwings and other shorebirds (Byrkjedal & Kålås, 1985; Redmond, 1986; Galbraith, 1988b; Šálek, 1995; Hegyi, 1996; Grønstøl, 1997; Hegyi & Sasvari, 1998; Sandercock *et al.*, 1999; Sharpe, 2006).

Three main not mutually exclusive factors can be responsible for this phenomenon: i) already depleted energy reserves during laying of replacement clutch (Hegyi & Sasvari, 1998) ; ii) younger females producing smaller eggs laying generally later in the season (Christians, 2002); and iii) lower food availability for females later in the breeding season. There are several indices, that female's food supply matters for the egg size and energetically rich earthworms play an important role (Baines, 1990; Grønstøl, 1997). For example, in South Sweden, lapwings arrived at their breeding grounds at the same time, but females at the sites with more earthworms started the egg-laying earlier (Högstedt, 1974). The more time proportionally spent by a female on arable land with better availability of earthworms before egg-laying, the bigger eggs were produced in their clutch consequently in another Swedish location (Blomqvist & Johansson, 1995). However, earthworms are later in the season less available as retreating deeper into the soil, particularly during dry weather conditions (Baines, 1990; Beintema *et al.*, 1991). Warmer winter and wetter spring can accelerate the start of lapwing breeding season (Both *et al.*, 2005; Musters *et al.*, 2010). Moreover, wetter early

spring could mean also more of easily available prey for females (Ausden *et al.*, 2001), which could be able to gather more energy and produce larger eggs than during dry conditions.

Habitat

Habitat is the influential predictor of lapwing egg size only at locations with a more polarized landscape with extensive coverage by one habitat and then the prevalence of the second habitat in different part of the study area. In Morocco, saline grasslands dominated at one site and wet meadows at the second site within the study area (Cherkaoui & Hanane, 2011). In other cases, eggs were found always bigger in arable land in comparison to coastal pastures (Blomqvist & Johansson, 1995), rough grazed pastureland (Galbraith, 1988b) or heathland (Murton & Westwood, 1974), which is in accordance with better earthworm availability at arable land (Blomqvist & Johansson, 1995). However, two studies (Blomqvist & Johansson, 1995; Cherkaoui & Hanane, 2011) reported smaller egg size in the habitat with higher proportion of replacement clutches and only two studies (Murton & Westwood, 1974; Galbraith, 1988b) had partial control for seasonality influence, therefore the overall effect of habitat size can be partially over-estimated and more driven by seasonality, similarly to findings in South Bohemia.

On the other hand, the effect of habitat on egg size in lapwing was not obvious in mosaic agriculture landscape consisting of heterogeneous mixture of arable fields with different crop types, meadows, pastures and fish ponds (South Bohemia, this study) or study areas consisting from grasslands only (Baines, 1990) or arable land only (Sharpe, 2006; East Bohemia). This finding is in line with the fact that females before egg-laying do not forage only at nesting site (Berg, 1993), on the contrary, the preference of foraging sites with the higher abundance of earthworms close to future nest sites was observed (Baines, 1990). Females can use for feeding the same "neutral fields" apart from their territories (Baines, 1990), therefore this possibility can easily reduce the effect of nesting habitat on egg size in the highly heterogeneous landscape. Habitats within arable land differed also in the egg size in our study, however only as a result of laying smaller eggs in replacement clutches in spring cereals after mechanical damage of bigger eggs in first clutches during agriculture management – harrowing of ploughed fields, not as a result of habitat per se. This finding also imply that future studies should implement simultaneous addressing of all possible predictors together in one model to be able to distinguish their relative importance.

Clutch size

There are no significant differences in egg size among 3-eggs and 4-eggs clutches. However, there was a slight tendency for larger clutches containing bigger eggs, being on average 0.9% larger (comparison between 3 and 4-eggs clutches). Moreover, reported significantly smaller eggs size in 2-eggs clutches fits into this pattern. Similarly, despite smaller sample sizes, also Galbraith (1988) found smaller egg volume in 2-egg clutches in comparison with larger clutches. But apart from Bohemian study locations, none from other studies account for the possible change of clutch size over the season (Shrubb, 2007), therefore it is important to treat the comparison among studies with caution.

Majority of bird species solve the „*trade-off*" between the number of eggs in the clutch and egg size (Blackburn, 1991; Figuerola & Green, 2006; Martin *et al.*, 2006), but this could not be the case for Northern Lapwing. The evidence gathered here suggests that individuals producing smaller clutch, do not have on the average more energy to make these eggs bigger. On the contrary, the egg size is generally smaller in these smaller clutches, at least in South Bohemia. Nevertheless, any egg size difference arising from 3 and 4-eggs clutches comparison is small and has only limited biological relevance.

Chick survival and conservation implications

Well known advantage of heavier shorebird chick hatching from bigger egg (Byrkjedal & Kålås, 1985; Galbraith, 1988b; Grant, 1991; Thompson & Hale, 1991; Hegyi, 1996; Blomqvist *et al.*, 1997; Hegyi & Sasvari, 1998; Dittmann & Hötker, 2001; Sheldon, 2002; Larsen *et al.*, 2003) was confirmed also for lapwings in South Bohemia. Besides the quality of parents (Blomqvist *et al.*, 1997), any initial advantage of larger size, even the small one, can be crucial for subsequent chick body condition, growth and survival (Galbraith, 1988b; Sheldon, 2002). In Scotland, chicks hatched from eggs bigger than 23 cm^3 had a twice better chance of survival until fledging than chicks from smaller eggs (Galbraith, 1988b), a similar advantage for bigger chick survival was apparent also in Sweden (Blomqvist *et al.*, 1997). Seasonal changes in the egg size, resulting in on average by 5.6% larger eggs and subsequently chicks at the beginning of the breeding season in comparison to its end can represent an important advantage promoting the chick survival and it is disproportionally larger than effects of nesting habitat or clutch size.

Similarly, food and water availability for chicks are on average deteriorated at the end of the breeding season (Matter, 1982; Galbraith, 1988a; Beintema *et al.*, 1991). Chick can try to compensate worsen food availability by more intense foraging activity but it means higher exposure to potential predators (Evans, 2004). Therefore conservation measures for lapwings should involve the presence of marshlands or shallow water pools with sparse vegetation – suitable foraging areas for chicks (Johansson & Blomqvist 1996; Ausden *et al.* 2003; Devereux *et al.* 2004; Eglington *et al.* 2008) and preservation of first breeding attempts, preventing clutch loses due to destruction by agriculture machinery. This can be achieved via direct nest protection (Kragten *et al.*, 2008; Zámečník *et al.*, 2018) or at larger scale with the use of effective agri-environmental schemes (Eglington *et al.*, 2010; Smart *et al.*, 2014; Schmidt *et al.*, 2017).

Northern Lapwing has undergone significant decline through Europe (BirdLife International, 2004; Delany *et al.*, 2009) and despite extensive efforts on changing this trend (e.g. Tucker *et al.*, 1994; Wilson *et al.*, 2009), the species is still declining (BirdLife International, 2015). Majority of lapwing populations either on grasslands or in landscape with predominance of arable fields is not able to produce sufficient number of fledged chicks to compensate for year-round adult mortality (Peach *et al.*, 1994; French *et al.*, 2000; Sheldon, 2002; Sharpe, 2006; Roodbergen *et al.*, 2012) and chick survival may play a pivotal role (Roodbergen *et al.*, 2012).

In conclusion, bigger eggs, together with the fact that food is more available for chicks at the beginning of the breeding season, represent the double advantage of first breeding attempts for lapwing chicks, from the population dynamics as well as conservation point of view. Simultaneous protection of first clutches together with maintenance of suitable food supply and water presence during the breeding season for adults and especially for chicks should be the target scenario in conservation measures for shorebirds breeding in the agricultural landscape.

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TABLES

Table 1. Description of nesting habitat categories in South Bohemia, Czech Republic.

Habitat category	Description
Ploughed field	Ploughed fields, stubble fields with partial ploughing
Meadow	Meadows and pastures
Winter crops	Winter wheat, oil-seed fields
Spring crops	Harrowed fields, spring crops, maize fields, spring beans
Clover	Clovers and temporal grass planting on arable land
Other	Fallow lands, dry fishpond bottoms, other marshlands, potatoes

Table 2. Effect of seasonality, clutch size and nesting habitat on mean egg size in the clutch. Linear mixed effect model with the random effect of year, all predictors were controlled for the effect of remaining ones (type III analysis, n = 1,125 clutches in 17 breeding seasons during 1988–2018 in South Bohemia, Czech Republic). Seasonality is expressed as standardized first day of incubation, see Methods for more details.

Predictor	χ^2	*df*	*P*
Seasonality	119.63	7,1	<0.001
Clutch size	9.33	7,3	0.025
Habitat	6.54	12,5	0.257

Table 3. Mean egg volumes and mean incubation start (first day of incubation for particular clutch) in four main four habitats (n = 1,043 clutches) in South Bohemia during 1988–2018. For detailed habitat descriptions see table 1.

Habitat	Mean egg volume (cm^3)	SE	Mean incubation start	SE (days)	*N*
Ploughed field	23.71	0.07	6 April	0.59	362
Meadow	23.56	0.11	2 April	0.55	147
Winter crops	23.49	0.10	4 April	0.59	167
Spring crops	22.97	0.07	27 April	0.94	367

Table 4. Review of seasonality, nesting habitat and clutch size influence on egg size among Northern Lapwing (*Vanellus vanellus*) populations. NA = no data available, ns = no significant relationship. NA/ns = reporting non-significant relationship but without exact data for the effect size calculation. Two main habitat categories are compared in each study. Only 3-eggs and 4-eggs clutches are compared in this table. Data for East Bohemia were collected by following the same methodology presented in this study. Relationships are expressed in percentage of the difference between mean values of tested categories from the overall mean egg size in the particular dataset (see Methods for details) and are directional for seasonality and clutch size but not for nesting habitat. Significant relationships (given by the significance presented in each study) are highlighted in bold.

Source	Location	Study period	Number of clutches (eggs)	Seasonality #	Habitat	Clutch size 3-4
this study, Šálek 1995	S Bohemia (CZ)	1988–2018	1,125 (4,384)	**(–6.8%)**	0.4% (ns)	+1.1% (ns)
our unpubl. data	E Bohemia (CZ)	2013–2018	119 (467)	**(–6.1%)**	1.3% (ns)	+0.3% (ns)
Baines 1990	N England (GB)	1986–1987	386	NA	0.2% (ns)	NA
Bellebaum & Dittberner 2001	NE Germany	2000	69 (252)	(–3.5%)	NA	NA
Blomqvist & Johansson 1995	SW Sweeden	1987–1990	216 (787)	–0.1%	**2.9%**	NA
Cherkaouki & Hanane 2011	N Morocco	2003–2010	69 (255)	NA	**3.1%**	NA
Galbraith 1988	S Scotland (GB)	1984–1986	220 (790)*	**–2.3%**	**2.9%**	+1.0% (ns)
Grønstøl 1997	W Norway	1991–1994	72 (288)*	**–11.8%**	NA	NA
Hart *et al.* 2002	SE England (GB)	1997	61 (226)	NA/ns	NA/ns	+0.9% (ns)
Hegyi 1996	C Hungary	1988–1995	34*	**–3.8%**	NA	NA
Klabník 1984	N Bohemia (CZ)	1975–1981	83 (318)	NA	NA	–0.8% (ns)
Murton & Westwood 1974	E England (GB)	1971–1973	55 (205)	NA	**6.0%**	NA
Parish *et al.* 2001	NE England (GB)	1992–1995	70*	**–4.0%**	NA	NA
Sharpe 2006	N Wales (GB)	2003–2004	274	**(–7.3%)**	NA/ns	NA/ns
Sheldon 2002	C England (GB)	1999–2000	190	**(–5.2%)**	NA/ns	NA/ns

* marked/individually recognized females - Seasonality means first vs. replacement clutches of the same females

first vs. replacement clutches or the regression through the whole season (in parentheses)

FIGURES

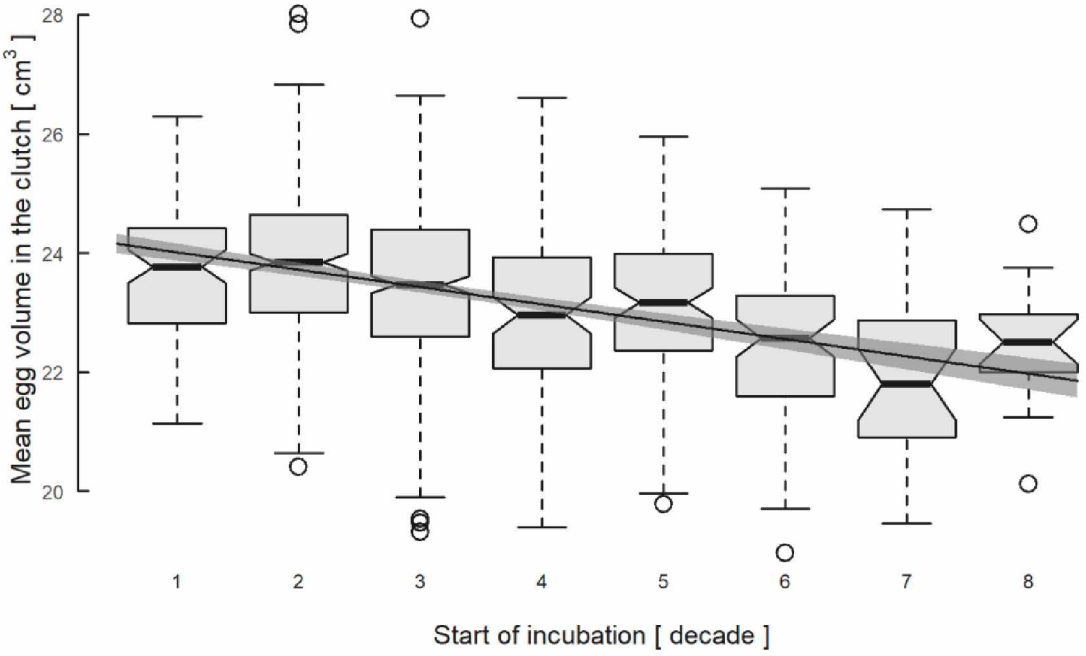

Figure 1. Mean egg volume in the clutch in relation to standardized first day of incubation. Line with shaded area indicates model prediction with 95% credible intervals based on the joint posterior distribution of 5 000 simulated values based on model outputs (table 2) and generated by the 'sim' function in R (Gelman *et al.*, 2016). Box-plots represent two decades before and six decades after the median of the first incubation day each year. Medians, quartiles, 1.5 inter-quartile range and outliers are presented, n = 1,125 clutches in 17 breeding seasons during 1988–2018 in South Bohemia, Czech Republic.

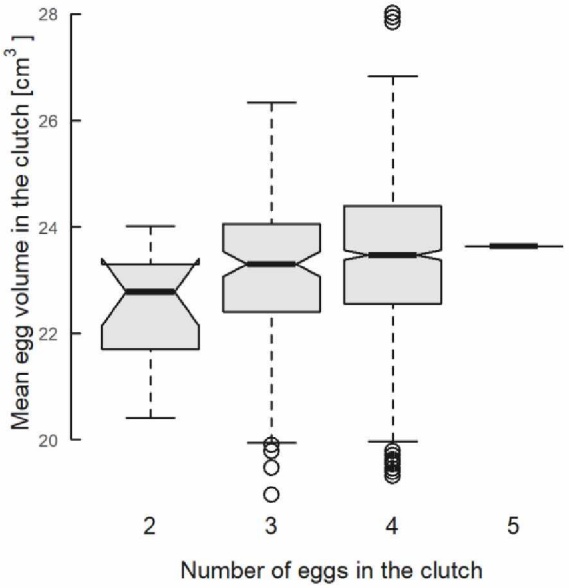

Figure 2. Mean egg volume in the clutch in relation to the clutch size. Medians, quartiles, 1.5 inter-quartile range and outliers are presented (overall n = 1,125 clutches, 4 eggs = 987 clutches, 3 eggs = 121 clutches, 2 eggs = 16 clutches, 5 eggs = 1 clutch) during 1998–2018 in South Bohemia, Czech Republic.

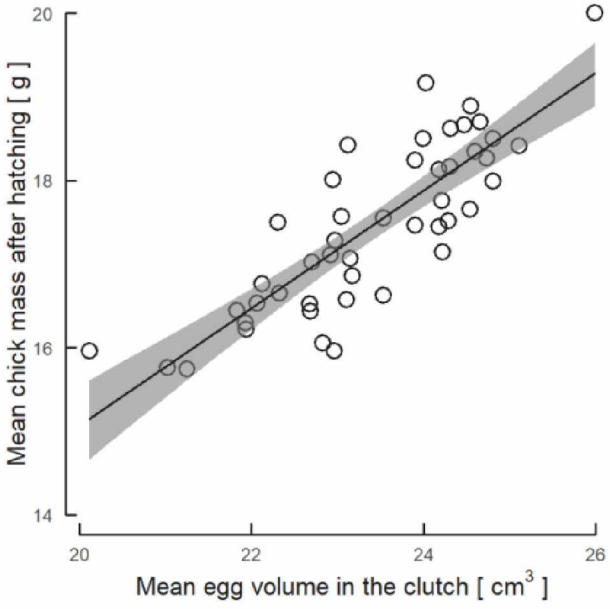

Figure 3. Relationship between mean chick mass at the day of hatching and mean egg volume. Line with shaded area indicates model prediction with 95% credible intervals based on the joint posterior distribution of 5 000 simulated values based on model outputs (table 2) and generated by the 'sim' function in R (Gelman *et al.*, 2016). Because we were not aware of hatching order of chicks, the mean chick body mass from all chicks in the clutch and the mean egg volume of all eggs in the clutch were used instead, each dot in the figure represents one family/clutch (n = 161 chicks from 46 clutches during 2013–2014) in South Bohemia, Czech Republic.

Direct nest protection of Northern Lapwing (*Vanellus vanellus*) nest in arable land, Czech Republic, 2014

Chapter 4

Visible marking of wader nests to avoid damage by farmers does not increase nest predation

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Visible marking of wader nests to avoid damage by farmers does not increase nest predation

VÁCLAV ZÁMEČNÍK, VOJTĚCH KUBELKA and MIROSLAV ŠÁLEK

Summary

Only a few studies have assessed the predation risk on artificially marked nests, or have examined ways of marking nests to avoid destruction by machinery. Until now, however, neither type of study has directly addressed this apparent trade-off experimentally. The impact of marking the nests of Northern Lapwing *Vanellus vanellus* with thin 2 m-long conspicuous bamboo poles with the top end highlighted with reflective red or orange spray has been tested for three years in two breeding areas of waders in the Czech Republic. A total of 52 pairs of nests on agricultural land, with each pair consisting of one marked nest and one unmarked reference counterpart nest, were monitored for 2004 nest-days until hatching, agricultural operations or failure. The results proved that marking itself does not result in increased nest predation. The nests found in the early incubation stage were under higher threat of depredation, irrespective of the presence of marking. Our results show that it is possible to find a finely-tuned trade-off in nest marking of ground-nesting birds between risk of damage by agricultural machinery and risk of increased nest predation. Our positive experience with Northern Lapwing, and episodically with three other wader species in the Czech Republic, suggests that this direct nest protection could be used effectively for a wider variety of ground-nesting birds.

Introduction

In most European countries the numbers of farmland birds have declined over recent decades (Chamberlain *et al.* 2000, Donald *et al.* 2001, 2006, Chamberlain and Vickery 2002, Butler *et al.* 2010, PECBMS 2013). There is an increasing evidence that one of the main problems for ground-nesting birds is low breeding success due to intensive agriculture and predation (e.g. MacDonald and Bolton 2008, Roodbergen *et al.* 2012). Several approaches to the elimination of nest destruction and depredation have been developed in many European countries, including various forms of direct nest protection (Guldemond *et al.* 1993, Isaksson *et al.* 2007, Kragten *et al.* 2008, Grüebler *et al.* 2012, Kentie *et al.* 2015, Santangeli *et al.* 2015, Sutherland *et al.* 2015). On meadows and arable land, the most widely-used technique is conspicuous marking to make the nest site visible to farmers operating machinery, e.g. with bamboo poles (Kragten *et al.* 2008, Schifferli *et al.* 2006, 2009). Farmers usually drive round the nest and leave a small part of the land undisturbed. The area of undisturbed land varies from several square metres in the case of waders and songbirds (Kentie *et al.* 2015, Schifferli *et al.* 2006; Grüebler *et al.* 2012) up to dozens of square metres in the case of Montagu's Harrier *Circus pygargus* (Kunstmüller and Kodet 2008). Direct protection is primarily applied to avoid nest destruction by farm machinery, but the use of relatively short poles just 1 m in height and inconspicuously coloured may not be sufficiently visible to farmers, and may therefore not be very effective in nest protection (Kragten *et al.* 2008). At the same time, marking itself has been considered to increase the risk of nest depredation (Kragten *et al.* 2008). However, the assumption about the risk of depredation of directly protected wader nests has never been properly verified experimentally.

The objective of our study was to investigate the use of long poles that are more visible to farmers and therefore more effective for direct protection of nests. It provides new findings from the Czech Republic, where the local population of Northern Lapwing *Vanellus vanellus* dropped by around 90% between 1982 and 2015 (Czech Society for Ornithology 2015). Most of this population breeds on arable land, where it is strongly dependent on farmland practices. As in other European countries, the main factors responsible for this decline are intensification of farming which includes irrigation, conversion of grasslands to arable, the development of agricultural machinery, increased use of pesticides and fertilisers (Fiala 2002, Šťastný *et al.* 2006, Kubelka *et al.* 2012a, Zámečník 2013), and predation of nests and chicks (Šálek 2000). On grasslands, the most high-risk operations are spring rolling and harrowing (Šálek 2000, Kubelka *et al.* 2012b); on arable land, the nests are often destroyed during cultivation of ploughed and fallow fields and when spring crops are sown (Kubelka *et al.* 2012a). Since 2009, direct protection of Lapwing nests has been one of the cross-compliance requirements. All farmers in the Czech Republic receiving direct payments are obliged to avoid destruction of nests when they have been officially informed about their position (Ministry of Agriculture of the Czech Republic 2015). This tool is still implemented only occasionally, but on traditional breeding sites it can be a crucial way of eliminating the destruction of clutches by farming activities. However, before this option can be promoted more widely among volunteers it is necessary to gather enough evidence that it is an effective measure and constitutes best practice. For this reason, the main objective of our study was to test experimentally whether marking the nests with two thin bamboo poles which would be visible enough to operating farmers affects the risk of predation on active Northern Lapwing nests. Our study aimed to provide evidence on whether nest marking of this type can be considered a safe conservation tool as regards the nest predation risk to ground-nesting birds in an agricultural landscape.

Methods

Data collection

Field work was carried out between 2010 and 2013 in two regions of the Czech Republic, one in South Bohemia (49.12N, 14.31E) and one in East Bohemia (50.18N, 15.61E), with a total area of about 500 km². In both regions, the dominant habitat is agricultural land, mainly a mosaic of arable (winter wheat, ploughed fields, spring cereal, oilseed rape, maize) interspersed with meadows, pastures (only in south Bohemia), linear non-cropped habitats along ditches and roads and, especially in south Bohemia, fishponds. The main potential nest predator species (red fox *Vulpes vulpes*, beech marten *Martes foina*, pine marten *M. martes*, stoat *Mustela erminea*, weasel *M. nivalis*, European hedgehog *Erinaceus europaeus*, Marsh Harrier *Circus aeruginosus* and Carrion Crow *Corvus corone*) are identical for these two areas (own observations and data from cameras placed at the nests).

Northern Lapwing breeding sites were determined on the basis of the conspicuous display and courtship behaviour of birds (e.g. Cramp and Simmons 1983) from the second half of March until the end of May. Nests were located either visually with the use of binoculars and spotting scopes, or by direct inspection of densely populated fields by a skirmish line with 5–8 (max. 12) observers (Kubelka *et al.* 2012b). The positions of the nests that were found were stored in a GPS tracker. All nests were marked with a thin willow twig 50 cm long fixed 15 m from the nest, exactly as in Šálek and Šmilauer (2002). This inconspicuous marking was found not to affect nest survival (Galbraith 1988). The incubation stage was assessed using a flotation test (van Paassen *et al.* 1984). When more than one nest was found in the same type of habitat and with a similar incubation stage and position within the field, pairs of nests were established and one (randomly selected) of the nests was provided with bamboo poles. Paired nests were chosen to be approximately 50–200 m away from each other. The bamboo poles were 2 m in length, 2–3.5 cm thick at the base, and 1 cm thick at the top. The top end was highlighted with a reflective red or orange spray.

The sprayed part of the bamboo was 15–20 cm in length. The bamboo poles were fixed along the line of cultivation 10–12 m apart, with a nest in the middle.

Our experiment was designed exclusively to test nest predation risk, i.e. nest pairs were situated in fields where no immediate farming activity was expected. Nevertheless, farmers were informed about the position of poles and if we were informed about an unexpected farming operation that could cause nest destruction, the experiment ended just before this operation (as control nests were also protected by bamboo poles). Both paired nests were repeatedly visited on the same day at irregular intervals, with a median of seven days (minimum two days and maximum 18 days), until the final fate of any of them was determined. Nests were recorded as successful when at least one egg hatched. Eggs were assumed to have hatched successfully when chicks or small remnants of eggshell were present in the nest (Green *et al.* 1987). Nests were assumed to have failed when no eggs hatched. If a nest was found empty, without eggshell remnants, or with large pieces of eggshell nearby, the nest was recorded as depredated. If there were signs of recent farming operations, and remnants of the nest were found, the nest was recorded as failed due to farming activities (three nests in two pairs, one nest even with bamboo poles). In our dataset, the losses were due only to predation and agricultural machinery; there was no desertion or other reason for failure. Once one of the nests was depredated or destroyed, the experiment on that pair was terminated. The date of predation was then calculated as the midpoint of the period between the last visit when eggs were present and the final visit. For the three nests (two pairs) destroyed by farm machinery, the experiment was terminated by the date of the last positive visit.

Data analysis

We used a paired t-test to test whether both marked and unmarked nests were equally distributed in respect to distance from the habitat edge. In order to assess whether the nests provided with poles also attracted predators toward the nest counterparts without poles, we compared the proportion of simultaneous predation events on both nests within nest pairs and proportion of predation events on just any one of the two nests within a pair. If the former prevails, we can assume significant attraction of poles for predators to both nests in a pair. The nest predation rate was calculated according to Mayfield (1975) as the proportion of the number of depredated nests and the sum of nest-day exposures. Hatching success reflected the daily survival rate powered by the mean incubation period of Northern Lapwing (27 days; Cramp and Simmons 1983).

A mixed-effect model (GLMM) with the chi-square testing procedure (likelihood ratio test, LRT) was applied to assess the fixed effects of poles, incubation stage, habitat, distances from the habitat edge and the interactions of the poles with all remaining predictors on the nest predation risk (response variable) expressed binomially (surviving = 1, predation = 0). Non-predation means a still active nest with eggs, or a hatched nest. The nest-specific incubation stage on the day when the experiment began might add to the explanation of nest depredation, so we included it in the model. As the locality might pseudo-replicate the predation risk of the same predators, we assigned nest pairs and breeding grounds as random effects. First we tested the effects of interactions, and after they had been removed we checked the contributions of the fixed effects (Crawley 2007). We adopted $\alpha = 0.05$ for the rejection of a hypothesis. We also checked the relationship between incubation stage on the day when the poles were installed and the day in the season (corrected by median date of incubation start in analysed nests within particular years). All statistical procedures were performed by 'lme4' package in R, version 3.1.2 (R Core Development Team 2014).

Results

A total of 104 nests in 52 pairs of nests in 15 localities, accounting for 2004 nest-days of exposure and 57 depredated nests were included in the analysis (Table 1). The distance from the nearest habitat edge of nests provided with poles [140 m ± (SE) 12.3 m] did not differ significantly from

Table 1. Dataset of nest pairs collected for various habitats in two areas in Bohemia.

Bohemia	ploughed field	maize	spring cereal	other
South	26	11	6	3
East	6	0	0	0

the control nests without poles [131 m ± (SE) 13.7 m] (paired t-test, $t_{51} = 1.4$, $P = 0.18$). The incubation stage on the day of the beginning of the experiment was identical for the nests provided with poles [nine days ± (SE) 0.8 days] and for the nests without poles [nine days ± (SE) 0.8 days] (paired t-test, $t_{51} = 0.2$, $P = 0.82$). Incubation stage was not correlated with day in the season (Spearman's rank correlation coefficient $r_s = -0.16$, $P = 0.10$).

The total daily nest predation rate was 2.8% ± (SE) 0.37%. The daily predation rate was 2.8% ± (SE) 0.54% in the marked nests ($n = 52$) and 2.8% ± (SE) 0.51% in the unmarked nests ($n = 52$), i.e. the hatching success was 47.0% for the marked nests and 44.8% for the unmarked nests. The mixed-effect model did not detect an effect of poles on the predation risk of the experimental nests (Table 2). The incubation stage was the only significant fixed effect; it showed that fresh nests were more prone to predation risk than nests closer to hatching date. As shown in Figure 1, nests found in the halfway incubation stage (14 days) still had about a 60% chance of survival while the nests found earlier had markedly reduced survival. We did not detect significant effects of habitat, distance from field edge or any interaction on nest survival, with the exception of the interaction poles × stage. This suggested that there were different effects of incubation stage in nests provided with poles and in nests without poles. A *post-hoc* analysis indicates that the nests without poles were more prone to depredation in the early stages of incubation (GLMM; estimate = 0.04 ± (SE) 0.011, $\chi^2 = 12.2$, $P < 0.001$) than the nests provided with poles (GLMM; $\chi^2 = 1.9$, $P = 0.17$). The proportion of simultaneously depredated nest pairs (40.4%) was not significantly higher than the number of predation events on one (28.8%) of the two paired nests (test of proportions, $\chi^2_1 = 1.1$, $P = 0.30$). We suggest that the poles did not affect simultaneous attraction to both nests within experimental pairs.

Discussion

Although marking of ground-nesting birds' nests for nest protection is generally used in many European countries, only a few studies have evaluated the effectiveness of this marking (Sutherland *et al.* 2015). Our experience indicates that, when applied in an optimal way, direct nest protection could be a suitable method for avoiding nest destruction during farming operations without raising the risk of nest depredation or desertion.

Probably the largest investigation was carried out in 2005 and 2006 in the Netherlands; this analysis included 1,644 protected nests against 229 nests without any protection (Kragten *et al.* 2008). The authors recorded a higher rate of predation of the marked nests in one study area

Table 2. Results of a mixed-effect model explaining the effects of the factors on the predation risk for the experimental Northern Lapwing nests. Ordered according to decreasing χ^2 values. A positive estimate means increasing survival.

Predictor	estimate	SE	χ^2	df	P
stage	0.04	0.007	20.867	1, 8	< 0.001
poles:stage	−0.02	0.012	3.841	1, 10	0.050
habitat	0.19	0.132	2.045	1, 8	0.153
poles	0.01	0.062	0.022	1, 8	0.882
poles:edge	−0.09	0.200	0.234	1, 10	0.628
edge	0.01	0.156	0.009	1, 8	0.925
poles:habitat	0.06	0.128	0.265	1, 10	0.607

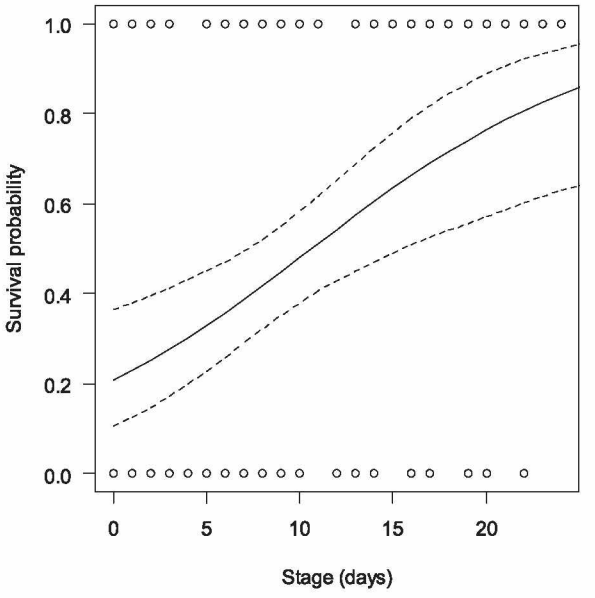

Figure 1. Probability (+95% CI) of nest survival (n = 104 nests) according to nest stage at the date of pole installation. All nests (provided with poles and without poles) are included.

during one season. They admit that the conspicuous markings may enhance nest predation in some circumstances. In addition, 6% of protected nests were destroyed due to farming operations. According to Götmark (1992), marking itself reduces nest destruction due to farming operations, but might attract predators through investigator disturbance. To avoid this potential bias, an experimental design based on pairing of nests, with only one of them marked and the other as a reference nest, was applied in our study. This design helped us to eliminate the effects of habitat, locality and to control the incubation stage at the date when the experiment started. However, our study has not revealed any impact of marking of nests on nest predation.

Timing of conservation action

Nests at earlier stages of incubation are under higher risk of predation as these include a group of poorly placed nests prone to be easily discovered by predators (Ricklefs 1969, Martin and Roper 1988, Eggers *et al.* 2005). An explanation that fresh Lapwing clutches were defended less intensively and thus were more exposed to predation risk is not supported by previous investigation (Kis *et al.* 2000). If these early clutches are marked for a longer time before field cultivation, subsequent losses due to predation will make this measure inefficient due to the unreasonable demands that it makes on farmers as these either unnecessarily drive around depredated nest or have to stop the tractor to check the nest. If it is depredated, drivers have to take away the bamboo poles before continuing their work.

A further risk connected with marking of early clutches is nest desertion. In Switzerland, half of the Lapwing nests marked with bamboo poles while eggs were being laid were deserted, probably due to sensitivity of females to disturbance of this kind in the early stages of nesting (Schifferli *et al.* 2009). This was probably aggravated by the relatively close placement of the poles, only 2–3 m from the nest. Also Kragten *et al.* (2008) recorded greater desertion of marked nests than of unmarked nests. As the nests in their study were marked immediately after they were found, clutches in the early stages of incubation were very likely also included. In our study,

nest marking did not result in any nest desertion, as bamboo poles were placed only when the clutches were complete. This indicates that clutches that are just being laid should be marked with poles only if field operations are imminent. If this is not possible, it is questionable whether the nests should be protected at all, having in mind the uncertain benefits of this measure in this particular case. Our finding that nests without poles were more prone to depredation in the early incubation stages than nests provided with poles we interpret as a type I error.

Optimal use of bamboo poles

In our experiment, poles were placed at least 5 m from the nest and there was no evidence of nest desertion. In previous studies, the poles were significantly closer (2–3 m in Switzerland, and 3–5 m in the Netherlands) and, as mentioned above, cases of nest desertion were relatively numerous. From the farmer's point of view, it makes practically no economic or technical difference whether the poles are placed 3 m or 5 m from the nest. Therefore to eliminate possible disturbance to the birds, poles should be placed at least 5 m from the nest.

In addition, it seems that taller poles that are sprayed with a bright colour at the top end are more effective than shorter poles with a natural colour. Altogether with this project, from 2010 until 2016 we used direct protection for more than 400 nests and all cases of nest destruction (up to 4% of protected nests) were due to a communication failure (own unpubl. data). It is therefore crucial to stay in close contact with farmers. They need to be informed without delay, and must be given precise information about the number of nests, the way in which they are marked and the dates of hatching. It is also useful to provide a map with the positions of the nests. It seems that the use of a bright reflective colour at the top of poles acts optimally for informed farmers, even if they are working at night (own unpubl. data), and that the bright reflective colour does not attract potential nest predators.

Direct protection has also been used with success for protecting a small number of nests of rarer waders breeding in the Czech agricultural landscape in the South Bohemian region (own unpubl. data) – several tens of nests of Little Ringed Plover *Charadrius dubius*, three nests of Black-tailed Godwit *Limosa limosa*, and one nest of Redshank *Tringa totanus*. These species easily accept marking of their nests with bamboo poles, and direct nest protection was highly successful.

Disadvantages of direct protection

Although our results did not show an increased rate of predation due to conspicuous nest marking to inform farmers, there is still a question of the learning abilities of some predators. It has already been confirmed that some predators are able to remember the position of an incubating individual, and they visit the breeding site when the parents are away (Šálek and Zámečník 2014). Corvids, in particular, are known to develop their predation tactics and to learn. Once these birds connect poles with possible prey, marking could lead to increased predation. Another risk arises with the possible attractiveness of the small plots around the nest that are created as a result of the tractor driver's efforts to avoid destroying a nest. This effect has already been proved for Montagu's Harrier (Koks and Visser 2000, Santangeli *et al.* 2015). To provide evidence of this, however, further specifically designed experiment is required.

In addition, it is not known how predators would respond to a high concentration of poles installed near to the nests in large breeding colonies concentrated around one hotspot (e.g. a piece of waterlogged land inside an arable field). We suggest that it would be more effective and technically more feasible in this case to protect the whole nesting colony from the risk of damage by farmers, rather than marking and avoiding each nest individually. In the long term, the best option is to adopt targeted agri-environment measures that would create an optimal breeding habitat and would prohibit any agricultural activity during the breeding season. However, a measure of this type should preferably be applied at regular breeding sites of local importance, and only if allowed by legislation and accepted by farmers.

Conclusion

Our results show that it is possible to find a finely tuned trade-off in marking the nests of ground-nesting birds between the risk of damage by agriculture machinery and the risk of increased nest predation. Two thin bamboo poles with the nest located between them are sufficiently visible for the farmer but, at the same time, they do not attract potential predators. Our positive experience with Northern Lapwing and episodically with three other wader species in a mosaic of arable plots and meadows in the Czech Republic suggests that this type of direct nest protection could be used effectively for a wider variety of ground-nesting birds. However, it is necessary to carry out further research on the responses of individual species to this kind of disturbance in association with depredation risk in larger colonies. Although direct nest protection can be used as a suitable protection tool, it is time-demanding and should be applied only when other conservation measures fail. Especially for regular breeding sites, it cannot effectively substitute a targeted large-scale conservation measure, e.g. an agri-environmental scheme.

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Northern Lapwing (*Vanellus vanellus*) chick hiding in a mosaic agricultural landscape, Czech Republic, 2013

Chapter 5

Threats and protection of meadow breeding shorebirds in the Czech Republic and Slovakia

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(in revision)

Threats and protection of meadow breeding shorebirds in the Czech Republic and Slovakia

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DEVELOPMENTS AND INTENSITY OF AGRICULTURE

Czech and Slovak agriculture landscape went through a quite complicated development with several meaningful twists in intensity and use of agriculture landscape during the 20th century (e.g. Andreska 1990, Šálek 2000, Albrecht 2015). Because Czech Republic (CZ) and Slovakia (SK) underwent the velvet divorce from former Czechoslovakia as late as 1993, developments and intensity of agriculture took place very similarly in both countries. Here follows the example of the CZ based on the summary presented by Albrecht (2015) with the input from other resources.

The area of agriculture land was persistently declining (by about 20%) during 1927–2008. The area of arable land was declining concurrently as well as the area of grasslands until the 1980's which has been continually increasing since then. The area of forest land increased by about 10% since the Second World War (Albrecht 2015). South Moravia represents a unique biogeographical region in the Czech Republic: it is warmer, drier, and generally flatter here than in the rest of the country. It also features highly fertile soil, and thus the region has long been a centre of agriculture. In South Moravia, there is 363,000 ha of cultivated agricultural land, of which 90% is arable land. The transformation of arable land to permanent grasslands (which take up an area of 19,000 ha) has occurred mainly in less fertile areas of the region, organic farming (4,900 ha in 2007) has developed mainly in regions with worse natural conditions, a total of 708 ha of agricultural land lay fallow (Vaishar et al. 2011).

Numbers of farm animals changed significantly during the focus period which had an imminent influence on the intensity and the way of agriculture land use. Numbers of cattle were significantly decreasing until 1960, then however increased nearly to the initial situation but then rapidly dropped to the less than half of the initial abundance. The conditions of cattle breeding changed significantly. Scattered small stable breeding prevailed up to 1950. Cattle could graze only at margin lands difficult to use in other way, meadows were only mowed and all mass was dried at the place. Concentrated big breedings with minimal use of grazing were set up during the later period of collectivization, the sillage production started at drained and aligned meadows. After 1990 most of the cattle was breeding freely at pasturelands, partially also during the winter. Numbers of horses decreased by about 93% during the focal period, numbers of sheep fluctuated significantly (Albrecht 2015).

SPECIES AND BREEDING HABITAT

The most updated population estimates, trends, threats and protection measures of five meadow breeding waders: Northern Lapwing (*Vanellus vanellus*) – VU, Black-tailed Godwit (*Limosa limosa limosa*) – CR, Common Redshank (*Tringa totanus totanus*) – CR/EN, Eurasian Curlew (*Numenius arquata arquata*) – CR and Common Snipes (*Gallinago gallinago gallinago*) – EN in the Czech Republic and Slovakia are covered in this article. Other European "grasslands waders" are not breeding in the region, therefore they are not present in this review. The legal status is the same in both countries for all species except Common Redshank which is considered as critically endangered in the Czech Republic, but as endangered in Slovakia (Danko 2002, Plesník et al. 2003, Hudec & Šťastný 2005).

Northern Lapwing, Black-tailed Godwit and Common Redshank, formerly more or less strictly meadow waders, are nowadays more commonly using arable land in CZ and SK for breeding (Danko 2002, Šálek 2000, Šťastný *et al.* 2006). The increase in agriculture intensification was followed by decline of breeding wader populations (Šťastný *et al.* 2006, Martiško 1994) and higher proportion of Northern Lapwings (Šálek 1990, 1994, Fiala 2002, Schröpfer 2002, Sťastný *et al.* 2006) and later also Black-tailed Godwits (Kubelka & Kadava 2014, Kubelka *et al.* 2016) started to use arable land, especially its wetter parts (field wetlands) as breeding habitat. There was recorded a decline in agriculture intensity around 1990 due to political changes but without noticeable positive effects on breeding farmland waders trends (Reif, Voříšek, Šťastný, Bejček, & Petr, 2008).

Arable land is predominant habitat for Northern Lapwing hosting more than 75% of breeding population in CZ on ploughed fields, winter wheat and spring crops, on the other hand, meadows and pastures host smaller proportion of breeding population (Kubelka, Zámečník, & Šálek, 2012a) with preference for ploughed fields in South Bohemia (Šálek 1990, Šálek 1994, Kubelka 2015). The last breeding Black-tailed Godwits in the whole region, in South Bohemian fishpond area near České Budějovice, are currently using equally arable land and meadows or pastures (Kubelka & Kadava 2014) sometimes also bottoms of fishponds (Kubelka & Pykal 2012). However predominant habitat for Black-tailed Godwit as well as Common Redshank was wet meadow until the end of 20th century (Šálek 1987, Martiško 1994, Bureš 1998, Kubelka *et al.* 2016). Generally, all waders use wetlands in the fields and meadows for breeding more often during wetter years and on the other hand slowly overgrowing bottom of fishponds during drier years (Čamlík *et al.* 2010, Kubelka & Pykal 2012, our unpubl. data).

Breeding Common Redshanks were closely monitored only in the fishpond area near České Budějovice and the breeding habitat was recorded for 76 certainly and probably breeding pairs during 2005–2016. Altogether fishpond bottoms or sludge lagoons were most commonly used (46%, 35 pairs), than arable land with marshlands (30%, 23 pairs) and the least often meadows or pastures (24%, 35 pairs). The shift towards the arable land is notable even during this period. Only 11% out of 38 pairs used fields during 2005–2010, however 50% out of 38 pairs of Redshanks used arable land for breeding during 2011–2016 (V. Kubelka, unpubl. data).

Eurasian Curlew is still a proper grassland breeder with nests only exceptionally found in arable land (Hudec & Šťastný 2005, Gahura 2010). The last regular breeding place was restricted to artificial grassland of Václav Havel airport in Prague (Šena 2013, Žďárek *et al.* 2015). All other traditional meadow breeding grounds have been abandoned, particularly due to improper using and human disturbance (Gahura 2010). The Common snipe is little bit different from previous species, because this species is not restricted to the lowland wet meadows, but can inhabit also middle and higher altitudes where prefers even smaller wetlands and peat bogs in forested landscape with tolerance of nearby trees and shrub presence (Šálek 2000, Šťastný *et al.* 2006).

NUMBERS, TRENDS AND DISTRIBUTION

Tab. 1. Current population estimates and trends of five wader species in the Czech Republic (CZ) and Slovakia (SK) See text for details.

Species	state	population estimate breeding pairs	long-term trend ca. 1970-2014	medium-term trend ca. 1970-1990	medium-term trend ca. 1990-2014	short-term trend ca. 2004-2014
Northern Lapwing	CZ	5,000-7,000	strong decline	strong decline	strong decline	moderate decline
Vanellus vanellus	SK	2,000-4,000	strong decline	?	?	?
Black-tailed Godwit	CZ	5-10	strong decline	strong decline	strong decline	strong decline
Limosa limosa	SK	0	strong decline	?	?	?
Common Redshank	CZ	25-40	strong decline	strong decline	strong decline	stable
Tringa totanus	SK	20-50	decline	?	?	?
Eurasian Curlew	CZ	0-1	strong decline	strong decline	strong decline	strong decline
Numenius arquata	SK	0	strong decline	?	?	?
Common Snipe	CZ	500-800	strong decline	strong decline	strong decline	?
Gallinago gallinago	SK	30-100	strong decline	?	?	?

Northern Lapwing is the most common shorebird species with the widest distribution in both countries: CZ 5,000–7,000 and SK 2,000–4,000 breeding pairs. Three detailed atlas mapping work periods: 1973–1977, 1985–1989 and 2001–2003 (Šťastný *et al.* 2006) in CZ based on the help of hundreds of volunteers provide a good estimate for population trend in the whole country. Approximately 20,000–40,000 pairs during 1985–1989 and only 7,000–10,000 pairs during 2001–2003 (Šťastný *et al.* 2006). According to the current detailed monitoring of lapwing breeding grounds in CZ during 2012–2016 (our unpubl. data) we estimate the current population approximately 5,000–7,000 breeding pairs. There is only one older estimate from whole country atlas mapping in SK: 2,500–5,000 breeding pairs up year to 2002 (Danko *et al.* 2002), the current estimate is 2,000–4,000 breeding pairs.

The long-term trend (*ca.* 1970–2014) is a strong decline in both countries (Fig. 1, Fig. 2, Danko *et al.* 2002, Šťastný *et al.* 2006, Žídková *et al.* 2007, Kubelka *et al.* 2012a, our unpubl. data). Where known, medium- and short-term trends also show strong declines (tab. 1), only in CZ the short-term trend (*ca.* 2004–2014) is stable or showing a moderate decline (our unpubl. data, ČSO 2017). Northern Lapwing is spread all over both countries apart from the high mountains in various habitats of the agricultural landscape (Fig. 3, Danko 2002, Šťastný *et al.* 2006, Kubelka *et al.* 2012a). Besides several estimates of lapwing nest survival in CZ (tab. 2), there is no thorough estimate of chick survival.

Black-tailed Godwit is the rare breeder in and CZ with only 5–10 breeding pairs (Kubelka & Kadava 2014), and the species is now gone from SK. Godwits have inhabited mainly grasslands (meadows and pastures) in lowlands of both countries, but the half of the population in CZ breeds nowadays on arable land (Kubelka &Kadava 2014, Kubelka *et al.* 2016). Long-, medium- and short-term trends are all strong declines for CZ (tab. 1), previous population estimates were 250–500 breeding pairs for 1973–1977, then only 30–60 pairs for 1985–1989 and 10–20 pairs for the period 2001–2003 (Hudec & Šťastný 2005, Šťastný *et al.*2006). There were 5–40 breeding pairs of godwits in SK before 2002 (Danko *et al.* 2002).

Tab. 2. Apparent nest survival and failure estimates for Northern Lapwing (*Vanellus vanellus*) from three localities in the different part of Bohemia. Other failures mean overgrowing in Plzeňsko, flooding and unknown nest failure in Českobudějovicko.

area	years	N nests	apparent survival and failure of clutches (% from all nests)					source
			hatched	predated	machinery	other	abandoned	
Českobudějovicko (South Bohemia, CZ) (GPS 49.1°N, 14.3°E)	1988–1991	267	60.4%	21.7%	13.9%	0.0%	3.0%	Šálek (1992)
Českobudějovicko (South Bohemia, CZ) (GPS 49.1°N, 14.3°E)	2011–2015	545	38.2%	47.9%	5.7%	2.0%	6.2%	our unpublished data
Plzeňsko (West Bohemia, CZ) (GPS 49.6°N, 13.2°E)	1992–2001	35	34.3%	42.9%	14.3%	8.7%	0.0%	Schröpfer (2002)
Královehradecko (East Bohemia, CZ) (GPS 50.2°N, 15.6°E)	2012–2014	119	53.5%	31.0%	11.6%	0.0%	3.9%	our unpublished data

Common Redshank is more or less equally abundant in CZ (25–40 breeding pairs) and SK (20–50). Redshanks inhabit mainly lowland partly-flooded pond-bottoms and also meadows and pastures in CZ and marshlands in arable land in CZ and SK. Long-term trends are a strong decline in CZ and a decline in SK. Medium-term trends are strong declines in CZ, the short-term trend in CZ is probably stable (tab. 1, Kubelka & Pykal 2012, Bureš 2015). Previous population estimates based on atlas mapping in CZ are 80–150 breeding pairs for 1973–1977, 40–60 pairs for 1985–1989 and 25–40 pairs for 2001–2003 (Hudec & Šťastný 2005, Šťastný *et al.* 2006) and numbers seem to be the same since then (Kubelka & Pykal 2012 Ždárek et al. 2015). There were 35–70 breeding pairs of Common Redshank in SK before 2002 (Danko *et al.* 2002). No demographic parameters are available for this species.

Eurasian Curlew is the very rare breeder in CZ (0–1). The species is now gone from SK. Curlews mainly inhabit grasslands (meadow and pastures) in lower elevations. Long-, medium- and short-term trends are strong declines in CZ as well as the long-term trend in SK (tab. 1). Previous estimates for CZ were 25–50 breeding pairs for 1973–1977, 5–15 pairs for 1985–1989 and 1–3 pairs for 2001–2003 (Hudec & Šťastný 2005, Šťastný *et al.*2006). Recently, there are occasionally seen pairs in suitable breeding habitat, but breeding was not confirmed for several years (ČSO & ČZU 2018). There were 3–30 breeding pairs of Eurasian Curlew before 2002 (Danko *et al.* 2002). Apparent nest survival from vanishing South Moravian population of this species during 1974–2001 was follows: from found 50 – mainly meadow clutches – 23 nests (46%) hatched at least one chick, 22 (44%) clutches were predated, one (2%) damaged by agriculture machinery and four (8%) abandoned. Chick survival was very low. From 140–150 breeding pairs in the area over the years, fledged juveniles were detected only in 15 cases. Majority of chicks was killed by mowing machinery and the rest by predators (Gahura 2010).

Common Snipes breeds regularly in both countries: CZ (500–800 breeding pairs) and SK (30–100). Common Snipes inhabit lowland grasslands (meadows and pastures) as well as peat-bogs in more forested landscapes at higher elevations. Long-term trends are a strong decline in CZ and SK;

medium- and short-term trends are also of the strong decline in CZ (tab. 1). Previous estimates were for CZ were 1,200–2,400 pairs for 1985–1989 and 500–800 pairs for 2001–2003 (Hudec & Šťastný 2005, Šťastný *et al.*2006). There exist no more updated estimate in CZ and it is difficult to judge whether the negative trend continues. There were 100–250 breeding pairs of Common Snipe in SK before 2002 (Danko *et al.* 2002). No demographic parameters are available for this species.

THREATS AND CONSERVATION

Northern Lapwing

Common threats to grassland-breeding lapwings in both countries and major factors driving these trends are: drainage of grasslands, conversion of grasslands to arable land and high fertilizer input in meadows leading to overgrowth and thick, poorly penetrable habitat, drilling of meadows during lapwing incubation period and grazing abandonment at fishpond margins (Šálek 1994, Šálek 2000, Danko 2002, Šťastný *et al.* 2006, Kubelka 2015) and fishpond cultivation intensification in CZ also play a role (Šálek 2000, Albrecht 2015).

Apart from indirect effects of agriculture intensification, there are key threats of nest and chick predation and direct damage by agriculture machinery. Predation is the most common failure of lapwing clutches in South Bohemia (Šálek 1992) (Šálek & Šmilauer 2002, Kubelka & Šálek 2013) (Kubelka 2015) as well as in West Bohemia (Schröpfer 2002) and East Bohemia (table 2). Larger breeding colonies in meadows experienced lower nest predation rate (M. Šálek & Šmilauer, 2002). Daily nest predation rate has increased over 25 years in fishpond area near České Budějovice (Fig. 9). Nest cameras have recorded two mammal predators: Stone Marten (*Martes foina*) and Red Fox (*Vulpes vulpes*) as the most important one (Kubelka 2015, Sládeček et al. unpubl. data). However, avian predators probably also play a role (Šálek & Cepáková 2006, Šálek & Zámečník 2014) and Klabník (1984) noted the Carrion Crow (*Corvus corone*) as only recorded predator of lapwing clutches in North Bohemia. Three avian predators: Marsh Harrier (*Circus aeruginosus*), Common Kestrel (*Falco tinnunculus*) and Long-eared Owl (*Asio otus*) were determined as chick predators in CZ (Kubelka 2015, Zámečník et al. unpubl. data).

Direct nest destruction by agriculture machinery is the common and widespread case of lapwing clutches failure (tab. 2). When a ploughed field is cultivated, the egg loss can reach 100% (our unpubl. data). It could be the same for meadows which are often drilled or rolled during the lapwing incubation period (Šálek 1992, Šálek 1994). Damage by agriculture machinery could be much higher without direct nest protection, e.g., in South Bohemia 37% of 52 nests would be damaged instead of real 14% in 2011 and 55% of 57nests instead of real 2% only in 2012 (Kubelka 2015). Therefore, we can assume that in CZ conventional agriculture landscape without any conservation measures, at least one third of all clutches is damaged by agriculture machinery every year.

Nest trampling by cattle is only a minor problem at few localities, where cattle is released to the pasture in the middle of lapwing incubation period (our unpubl. data). Other detected threat (based on the chick ringing data) is hunting pressure at wintering sites which have been found to be negatively connected to lapwing population trends in the different part of CZ (Žídková *et al.*2007).

Large-scale effective protection for lapwing on grasslands is generally lacking, however, protection in small-scale nature reserves (NR) can work well. Conservation measures in CZ consist of efficient small-scale measures (NR with a high water table) and direct nest protection against agriculture machinery (Kubelka *et al.* 2012b). This protection consists of two thin 2 m-long conspicuous

bamboo poles with the top end highlighted with reflective spray placed along the line of cultivation 10–12 m apart, with a nest in the middle. The measure works very well, it is adequately obvious for farmers, but the marking does not increase nest predation (Zámečník *et al.* 2018). An agri-environmental scheme for lapwings on arable land, consisting of the ploughed field left without any intervene through the breeding period (Zámečník 2014) seems to be promising after two years of being in practice, but exact evaluations have not been done yet.

Black-tailed Godwit

The main factors driving the declines are the same as for lapwing (Šálek 1987, Bureš 2012). Effective large-scale protection measures are generally lacking. Direct nest protection works well at last breeding grounds of this species in South Bohemia (Zámečník *et al.* 2018). Negotiation with fish farmers concerning the maintaining of the low water level in a fishpond after the Black-tailed Godwit or Common Redshank start of breeding on the fishpond bottom has been proved as an effective conservation measure (Kubelka & Pykal 2012).

Common Redshank

The main factors driving the declines are the same as for lapwing (Šálek 1987, Šálek 2000). Effective large-scale protection measures are generally lacking. Protection in CZ and SK consists of NR, direct nest-site protection is applied effectively for part of the population in South Bohemia, CZ (Zámečník *et al.* in 2018).

Eurasian Curlew

The main factors driving the declines are the same as for lapwing; another factor in CZ is the higher human disturbance at former breeding grounds (Gahura 2010). Effective large-scale protection measures are generally lacking. There are no protections measures in CZ, the last regular breeding site was the airport and the airport regime, paradoxically without human disturbance is probably the best protection.

Common Snipes

The conversion of meadows to arable land, drainage of wetlands, high fertilizer input and drainage of meadows are assumed to be the main threats in CZ and SK (Šálek 2000, Danko *et al.* 2002, Hudec & Šťastný 2005). AES on meadows in CZ working during 2004–2013 and consisting of postponed cutting regime only (Scharf, Slánská, & Tóthová, 2007) has not been properly evaluated, but it was probably ineffective as waders avoided these sites (V. Kodet in litt., our unpubl. data). Therefore this scheme application terminated in 2014. Protection in nature reserves with higher water table works well in some parts of CZ and SK as well as quite sophisticated restoration of former peat bogs (Lysák & Kodet 2016), where Common Snipe can work nicely as flagship and umbrella species (Kodet 2017).

FUTURE PERSPECTIVES

Meadow shorebirds are still generally declining in CZ and SK, however, at least in recent years, elevation of this trend seems to be apparent for few species. Apart from effectively working direct nest protection for various shorebird species (Zámečník *et al.* 2018), revitalisation of peat bogs is beneficial for Common Snipe (Lysák & Kodet 2016) and can serve as an inspiration for future

revitalisation projects. Another conservation measure, successfully promoting meadow shorebirds consists of leaving of a fishpond at the low water level through the whole breeding season. This prescription works very well, however, negotiation with fishermen is difficult and rarely successful (Sychra *et al.* 2008).

As a very promising seems to be the new agri-environmental scheme launched for Northern Lapwing at arable land in CZ. This prescription consists of the non-managed ploughed field during the whole breeding season, preferably at traditional and waterlogged breeding grounds (Zámečník 2014), which is very similar to the German scheme (Schmidt *et al.* 2017). The recent comparison of agro-environmental scheme plots with the control sites (also breeding grounds suggested for the prescription but farmer declined it) suggests, that the scheme does not only promote the higher abundance of Northern Lapwing in comparison with control plots but attract also otherwise very rare shorebirds in CZ, the Common Redshank and Black-tailed Godwit. Other farmland birds as e.g. Eurasian Skylark (*Alauda arvensis*) together with butterflies and bumblebees benefit from the scheme (our unpubl. data). Northern Lapwing works nicely as the "umbrella species" in this case, however, thorough evaluation, together with whole breeding productivity assessment for Northern Lapwing is needed.

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FIGURES

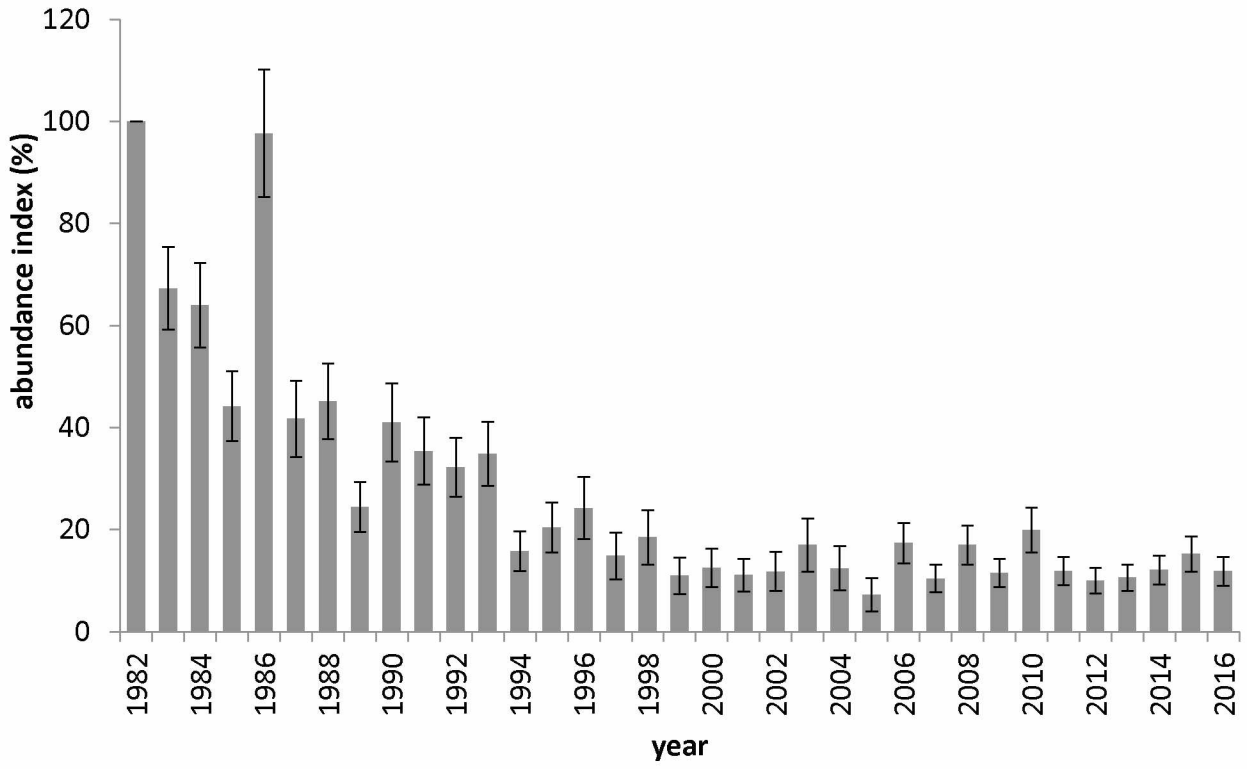

Fig. 1. Trend of the abundance of Northern Lapwing (*Vanellus vanellus*) with 95% confidence intervals, based on the JPSP in the Czech Republic (ČSO 2017) since 1982 (100%).

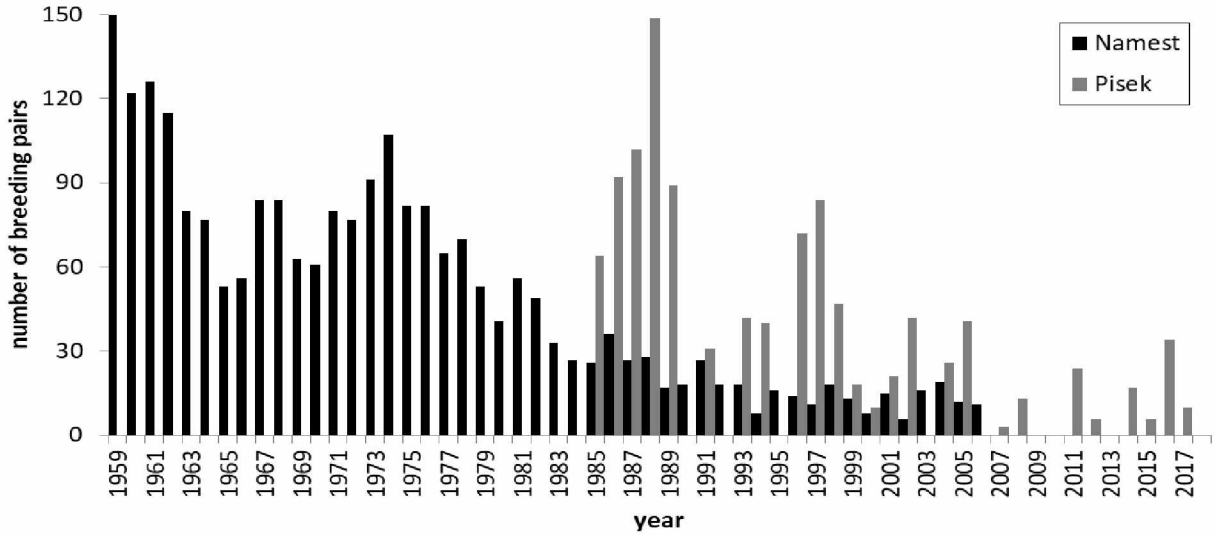

Fig. 2. Trend of the abundance of Northern Lapwing Lapwing (*Vanellus vanellus*) in numbers of breeding pairs at "Namest" (centre: 49.2°N, 16.2°E) in "Vysočina" disctrict (Fiala 2002) and "Pisek" (M. Šálek unpubl. data) in South Bohemia (centre: 49.2°N, 14.1°E), both in the Czech Republic. Covered regions differs in size. Empty years in Pisek region mean no monitoring in the particular year.

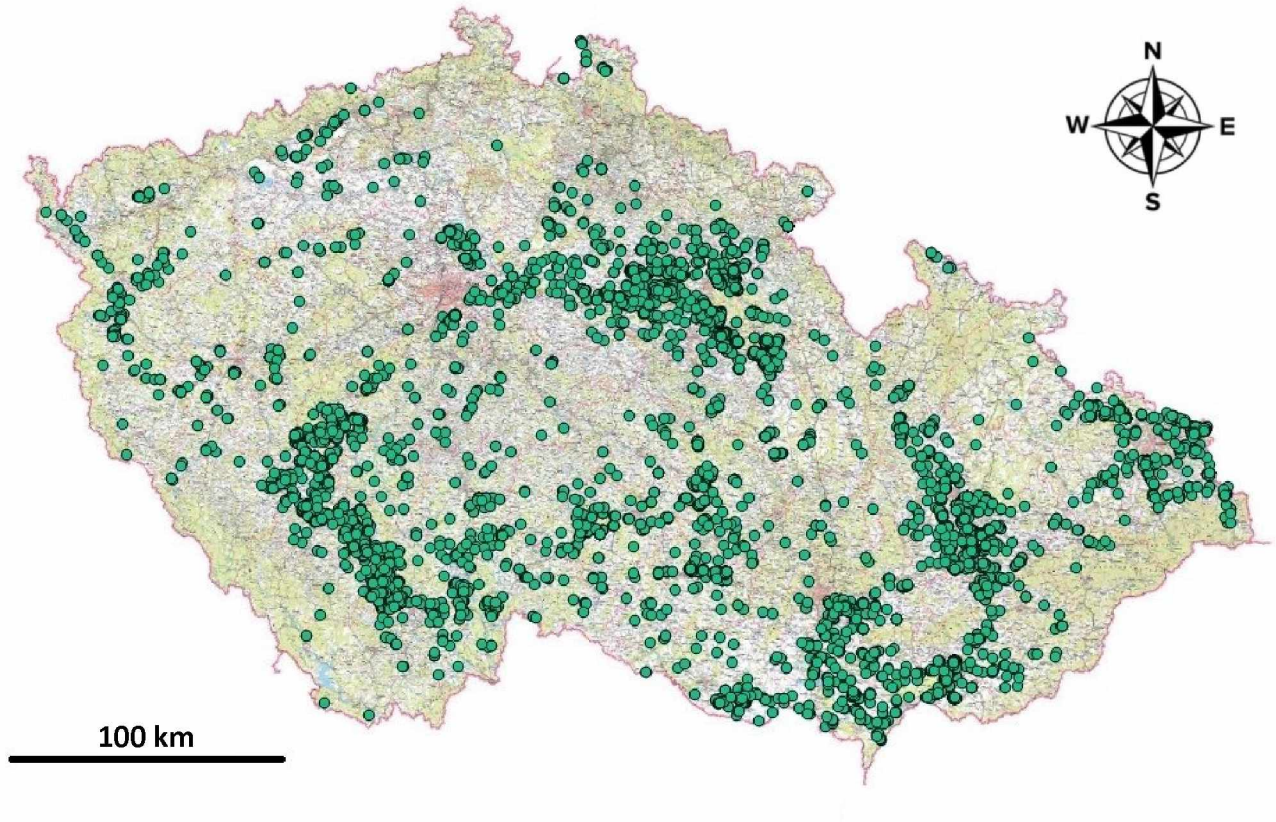

Fig. 3. Distribution of lapwing breeding grounds in the Czech Republic based on the volunteer monitoring during 2012–2018. N = 4,972 visits of particular breeding grounds, many of them repeatedly (ČSO and our unpubl. data)

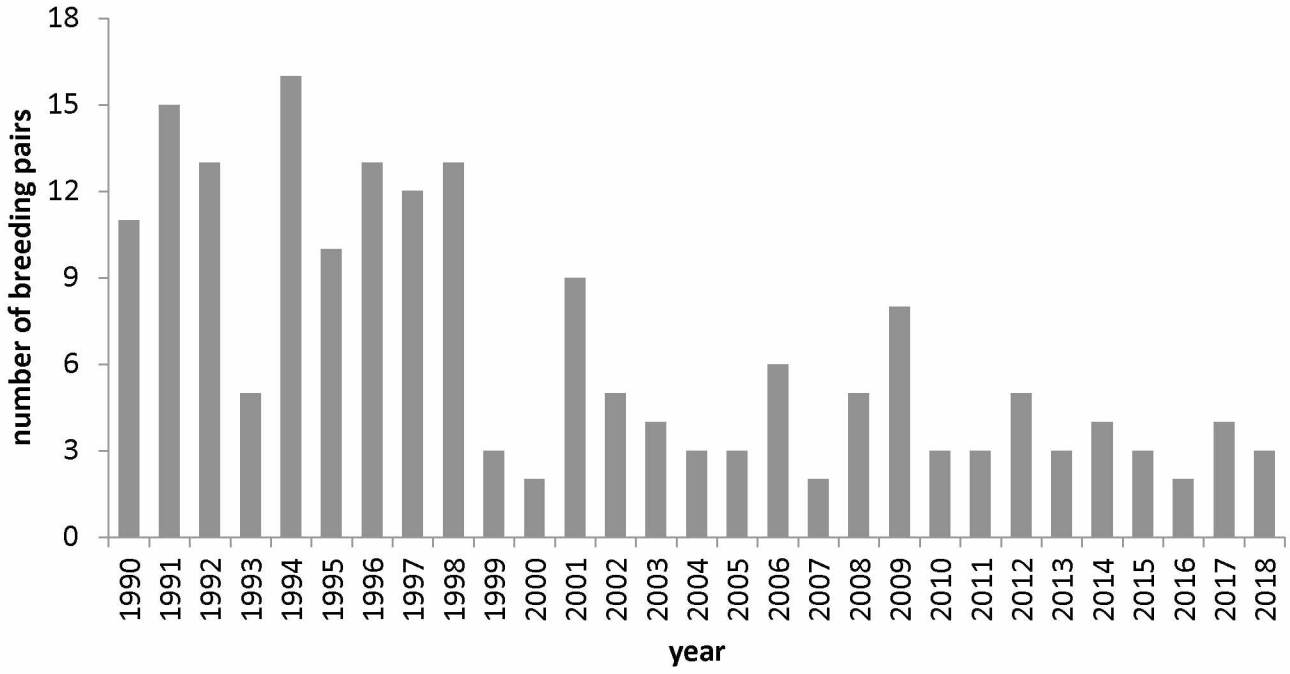

Fig. 4. Trend of the abundance of Black-tailed Godwit (*Limosa limosa*) in IBA Českobudějovické rybníky (centre: 49.0°N, 14.3°E) in the South Bohemia in the Czech Republic during 1990–2016. These are surely and probably breeding pairs only. Adapted from (Bureš 2012, Kubelka & Kadava 2014, Kubelka *et al.* 2016 and V. Kubelka unpubl. data).

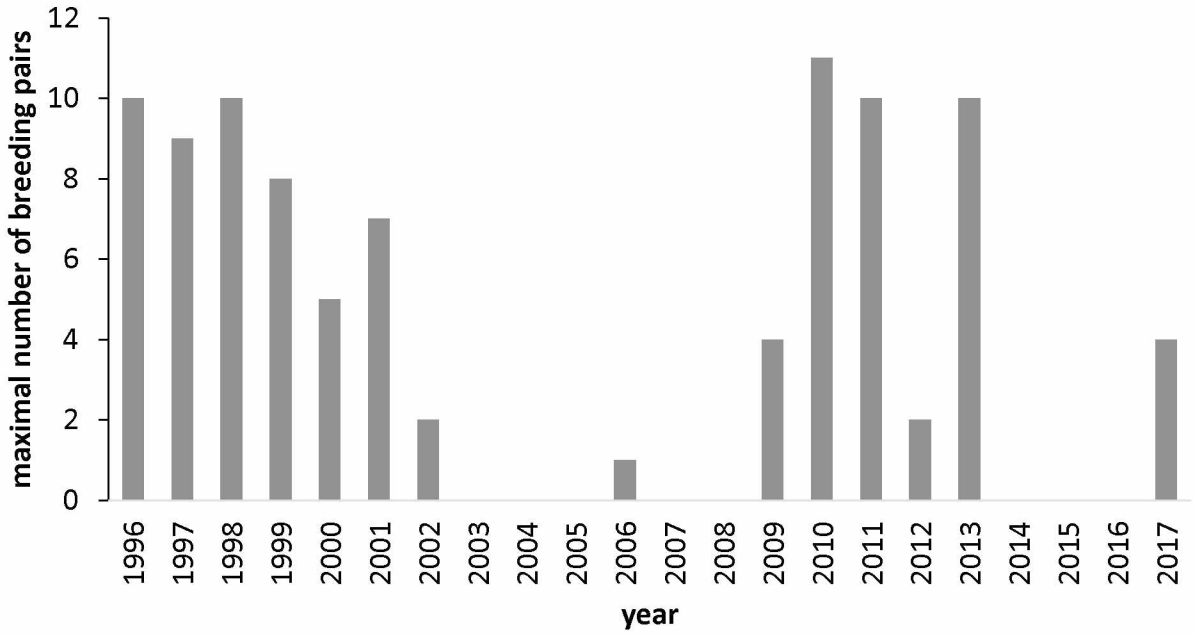

Fig. 5. Trend of the abundance of Common Redshank (*Tringa totanus*) in IBA Poiplie in the Central South Slovakia during 1996–2017. Maximum number of possibly breeding pairs is presented (Mojžiš *et al.* 2011, M. Mojžiš, D. Kerestúr, R. Václav unpubl. data).

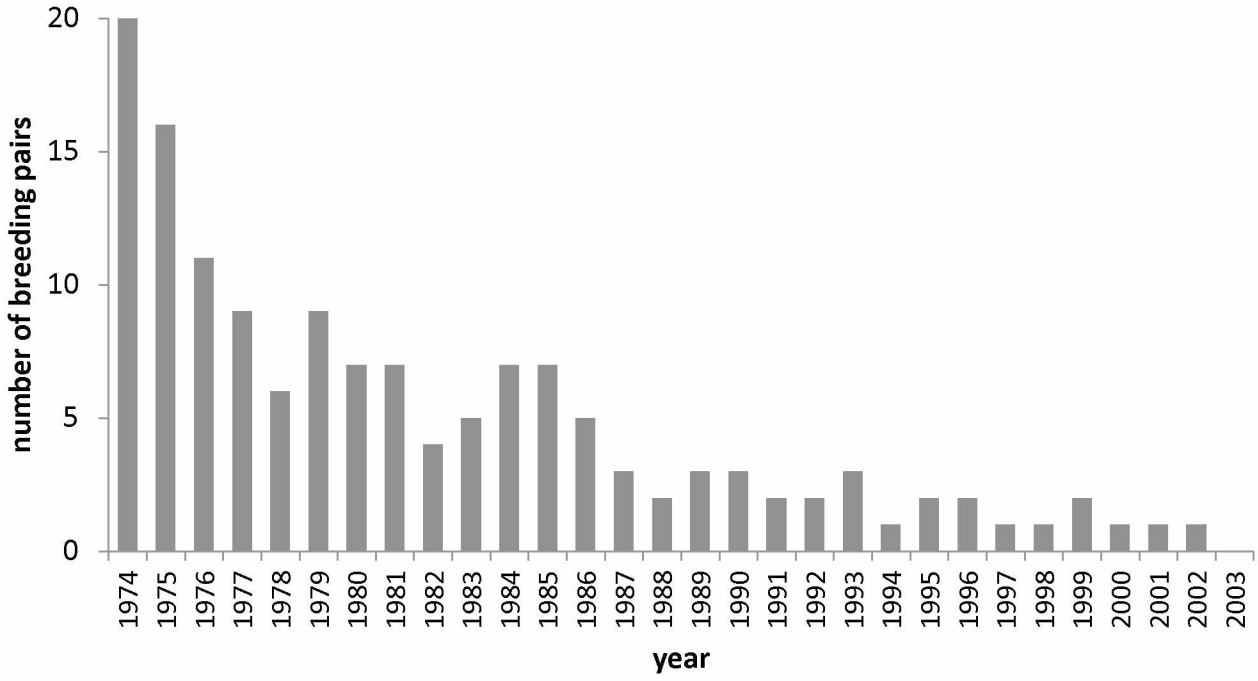

Fig. 6. Trend of the abundance of Eurasian Curlew (*Numenius arquata*) in South Moravia (centre: 48.9°N, 17.3°E) in the Czech Republic during 1974–2010. These are surely and probably breeding pairs only. There was one non-breeding pair in 2003 and no breeding curlews were recorded afterwards (Gahura 2010).

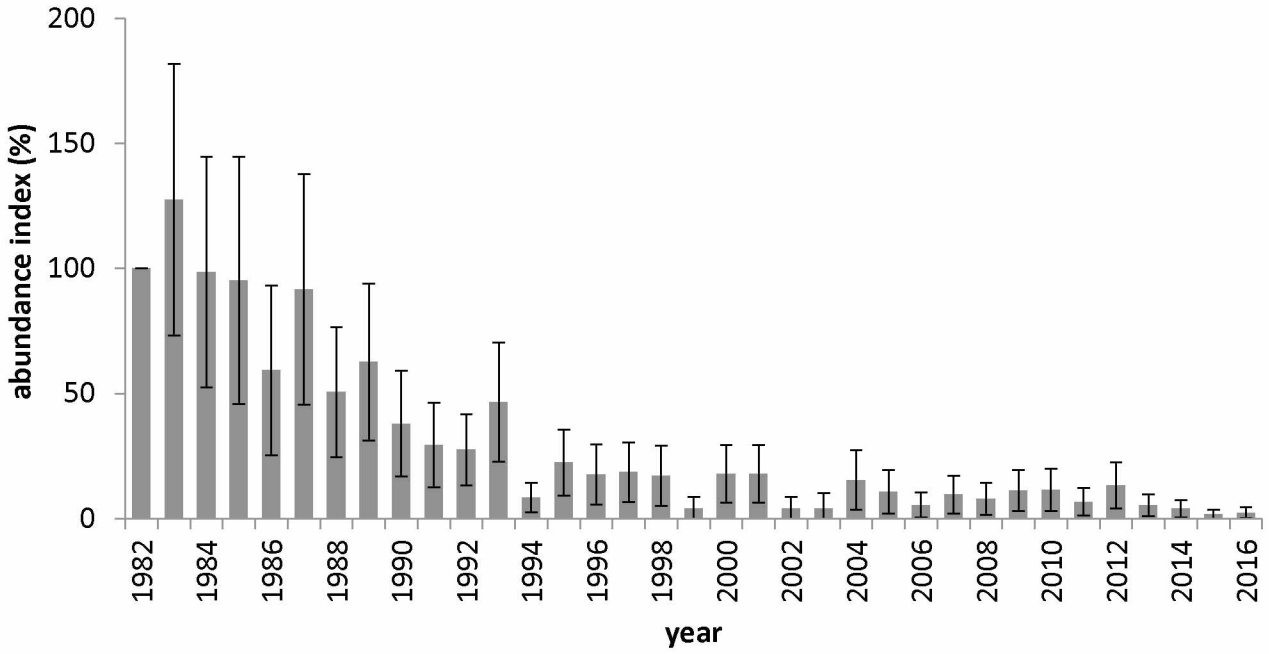

Fig. 7. Trend of the abundance of Common Snipe (*Gallinago gallinago*) with 95% confidence intervals, based on the JPSP – the common bird monitoring scheme in the Czech Republic (ČSO 2017) since 1982 (100%).

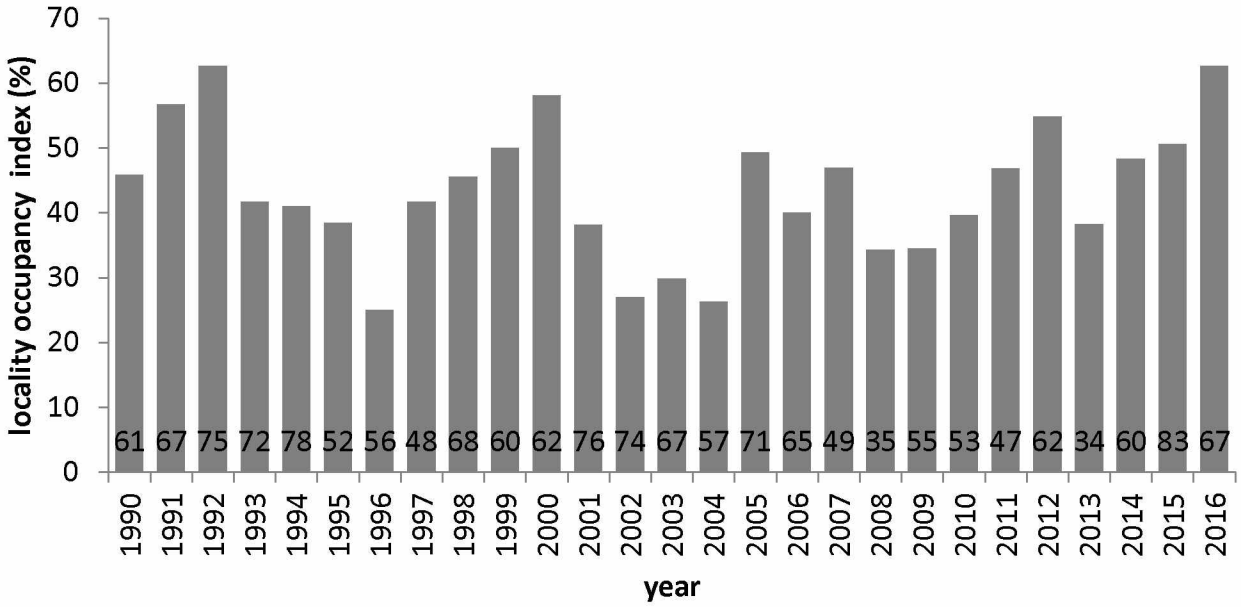

Fig. 8. Locality occupancy by at least one Common Snipe (*Gallinago gallinago*) in Vysočina district (centre: 49.5°N, 15.6°E) in the Czech Republic during 1990–2016. Number of monitored localities each year is given in the base of the particular bar (V. Kodet unpubl. data).

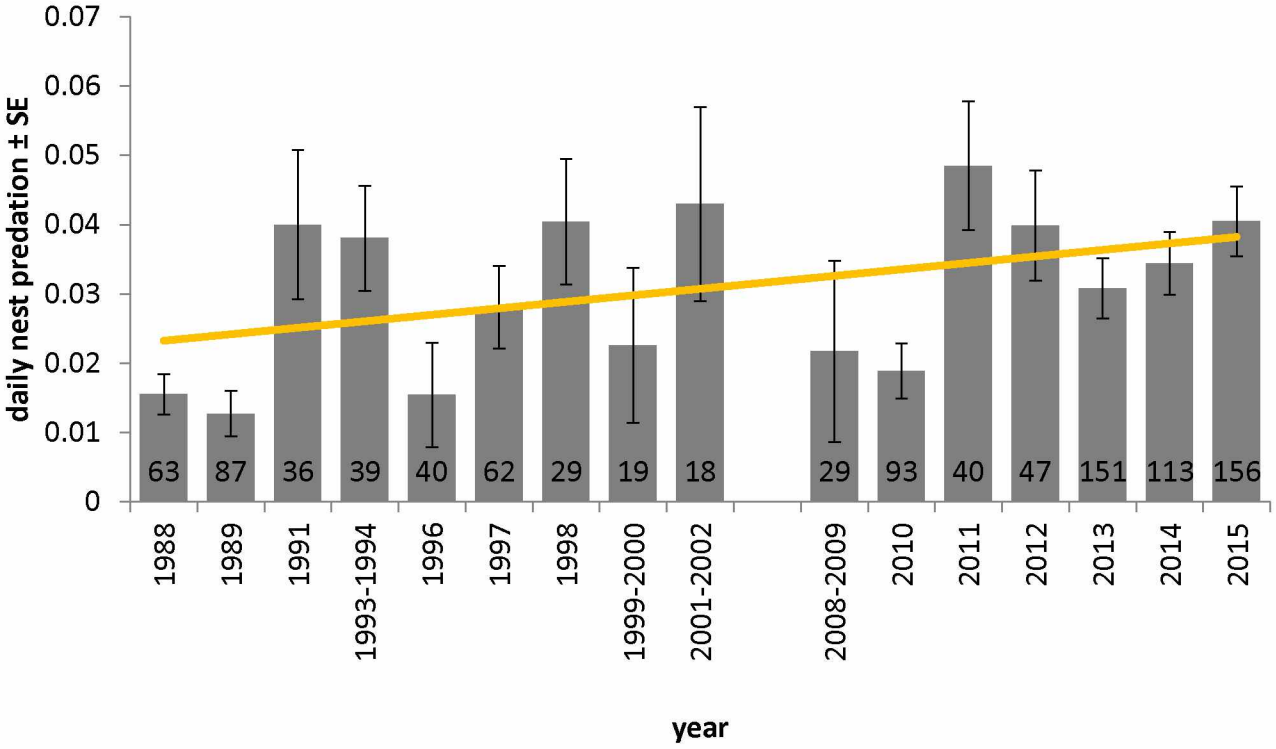

Fig. 9. Daily predation rate of Northern Lapwing (*Vanellus vanellus*) nests near České Budějovice (centre: 49.1°N, 14.2°E) in South Bohemia, Czech Republic. Daily nest predation computation follows Mayfield's (1961, 1975) approach with SE computation according to Johnson (1979). Sample sizes (number of nests involved) are given in the base of the particular bar.

Clutch and chick of Litttle Ringed Plover (*Charadrius dubius*) in a ploughed field, Czech Republic, 2013

Chapter 6

Inter-spefific nest scrape reuse in waders: Little Ringed Plovers taking over the nest scrapes of Northern Lapwings

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SHORT REPORT

Inter-specific nest scrape reuse in waders: Little Ringed Plovers taking over the nest scrapes of Northern Lapwings

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Capsule Inter-specific nest scrape reuse is rare in waders. We review this phenomenon and document it for the first time in the Little Ringed Plover *Charadrius dubius* breeding in vacant nest scrapes excavated by Northern Lapwings *Vanellus vanellus*.

Waders (Charadrii) usually excavate a simple nest scrape and line it sparsely with material from surroundings (del Hoyo *et al.* 1996) to be as inconspicuous as possible for predators but also to provide good thermoregulation at the same time (Reid *et al.* 2002, Mayer *et al.* 2009, Tulp *et al.* 2012). Only two species regularly use nests built by other birds (Green Sandpiper *Tringa ochropus* and Solitary Sandpiper *Tringa solitaria*) and two occasionally (Grey-tailed Tattler *Tringa brevipes* and Wood Sandpiper *Tringa glareola*), especially the abandoned forest nests of thrushes (Oring 1973, Cramp 1983, Pulliainen & Saari 1991, del Hoyo *et al.* 1996).

Creating a new nest scrape for breeding is probably not energy demanding (Amat *et al.* 1999) and old nest scrapes are often left unused even if they are available in the breeding territory (Gratto *et al.* 1985). In addition, the process of excavation has been described as an important part of the courtship ritual prior to copulation (Cramp 1983). Nevertheless, there are many examples of reuse of the nest scrape by the same or different individuals in several wader species within the same or in the subsequent breeding season. The Birds of North America database (Poole 2013) refers to intra-specific nest scrape reuse in 26 out of 50 American wader species, and it has been widely documented elsewhere (Parr 1980, Cramp 1983, Amat *et al.* 1999, Soloviev *et al.* 2001, Bertolero 2002, Schekkerman *et al.* 2004), but it occurs only at low frequency (Poole 2013). In contrast, use of the nest scrape by different wader species (inter-specific reuse) has been recorded only exceptionally (Table 1 containing all the records we could find). Here we document its occurrence in two European species, the Little Ringed Plover *Charadrius dubius* and Northern Lapwing *Vanellus vanellus*.

The Little Ringed Plover is a common wader species distributed widely across Europe (BirdLife International 2004, Delany *et al.* 2009). It primarily breeds in habitats dominated with bare ground and low sparse vegetation close to water, including human-altered environment such as the bottoms of dry ponds, sandpits and other post-industrial sites (Cramp 1983, Parrinder 1989, del Hoyo *et al.* 1996, Fojt *et al.* 2000). In the Czech Republic in addition to these habitats (Hudec & Šťastný 2005, Šťastný *et al.* 2006), arable land, especially freshly sowed maize fields and parts of wet fields with sand or gravel, seem to be another important breeding habitat for the species, at least in South Bohemia in recent years (Cepáková *et al.* 2007, Kubelka unpubl. data). In the Little Ringed Plover, the male usually excavates several nest scrapes that are subsequently lined with small stones and pieces of vegetation, and the female chooses one of these during courtship (Walters 1956, Cramp 1983, Hudec & Šťastný 2005).

During a study of a Northern Lapwing (hereafter lapwing) population in South Bohemia, Czech

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Table 1. Inter-specific nest scrape reuse in waders.

Reused by	Built/excavated by	When reused[a]	*n* of cases	References
Black-necked Stilt *Himantopus mexicanus*	American Avocet *Recurvirostra americana*	probably 0	more than 1	Robinson *et al.* (1999)
American Avocet *Recurvirostra americana*	Black-necked Stilt *Himantopus mexicanus*	probably 0	more than 1	Robinson *et al.* (1999)
American Golden Plover *Pluvialis dominica*	Stilt Sandpiper *Calidris himantopus*	2	1	Moitoret *et al.* (1996)
Pacific Golden Plover *Pluvialis fulva*	American Golden Plover *Pluvialis dominica*	1	1	Johnson *et al.* (2007), Johnson & Connors (2010)
Little Ringed Plover *Charadrius dubius*	Northern Lapwing *Vanellus vanellus*	0	2	this study
Lesser Sand Plover *Charadrius mongolus*	Red Knot *Calidris canutus*	1	1	P. Tomkovich (pers. comm.)
Hudsonian Gotwit *Limosa haemastica*	Short-billed Dowitcher *Limnodromus griseus*	0 or 1	1[b]	Walker *et al.* (2011)
Ruff *Philomachus pugnax*	Dunlin *Calidris alpina*	2	1	Soloviev *et al.* (2001)
	Pectoral Sandpiper *Calidris melanotos*	1	3	Soloviev *et al.* (2001)
	Red Phalarope *Phalaropus fulicarius*	1 and 4	2	Soloviev *et al.* (2001)
Curlew Sandpiper *Calidris ferruginea*	Dunlin *Calidris alpina*	1	1	Soloviev *et al.* (2001)
Dunlin *Calidris alpina*	Pectoral Sandpiper *Calidris melanotos*	3	1	Soloviev *et al.* (2001)
	Red-necked Phalarope *Phalaropus lobatus*	0	1	Gratto *et al.* (1985)
Little Stint *Calidris minuta*	Pectoral Sandpiper *Calidris melanotos*	1	3	Soloviev *et al.* (2001)
Least Sandpiper *Calidris minutilla*	Semipalmated Sandpiper *Calidris pusilla*	not known	1	Gratto *et al.* (1985)
Pectoral Sandpiper *Calidris melanotos*	Ruff *Philomachus pugnax*	1 and 2	2	Soloviev *et al.* (2001)
	Dunlin *Calidris alpina*	1 or 2 ; 2	2 ; 1	Moitoret *et al.* (1996), Soloviev *et al.* (2001)
	Red Phalarope *Phalaropus fulicarius*	not known	1	Soloviev *et al.* (2001)
Semipalmated Sandpiper *Calidris pusilla*	Dunlin *Calidris alpina*	1	1	Gratto *et al.* (1985)
	Red-necked Phalarope *Phalaropus lobatus*	not known	4	Gratto *et al.* (1985)
Red-necked Phalarope *Phalaropus lobatus*	Semipalmated Sandpiper *Calidris pusilla*	1	1	Gratto *et al.* (1985)
Red Phalarope *Phalaropus fulicarius*	Pectoral Sandpiper *Calidris melanotos*	2 and 3	2	Soloviev *et al.* (2001)
	Dunlin *Calidris alpina*	1	1	J. Hansen (pers. comm.)
Willet *Tringa semipalmata*	Marbled Gotwit *Limosa fedoa*	1	1[c]	Lowther *et al.* (2001)

[a]0 = Nest scrape reused in the same year, 1 = nest scrape reused in the next year, 2 = nest scrape reused after two years (one year gap in usage), 3 = nest scrape reused after three years (two years gap in usage), 4 = nest scrape reused after four years (three years gap in usage), some numbers were completed by M. Soloviev (pers. comm.).
[b]appropriation of nest with dowitcher eggs, nest ultimately held eight eggs: four godwit and four dowitcher, although the dowitcher eggs were eventually pushed to the side and left unincubated, it is not known if these dowitcher eggs were from that year or the previous year.
[c]only rescraped, but another scrape nearby was used for egg-laying.

Republic, we found two clutches of Little Ringed Plovers (hereafter plover) on 21 April 2013, placed in nest scrapes excavated by lapwings. The plover nests were placed 125 m apart from each other within a lapwing breeding colony (24 m and 11 m from the nearest active lapwing nests, respectively) consisting of ten

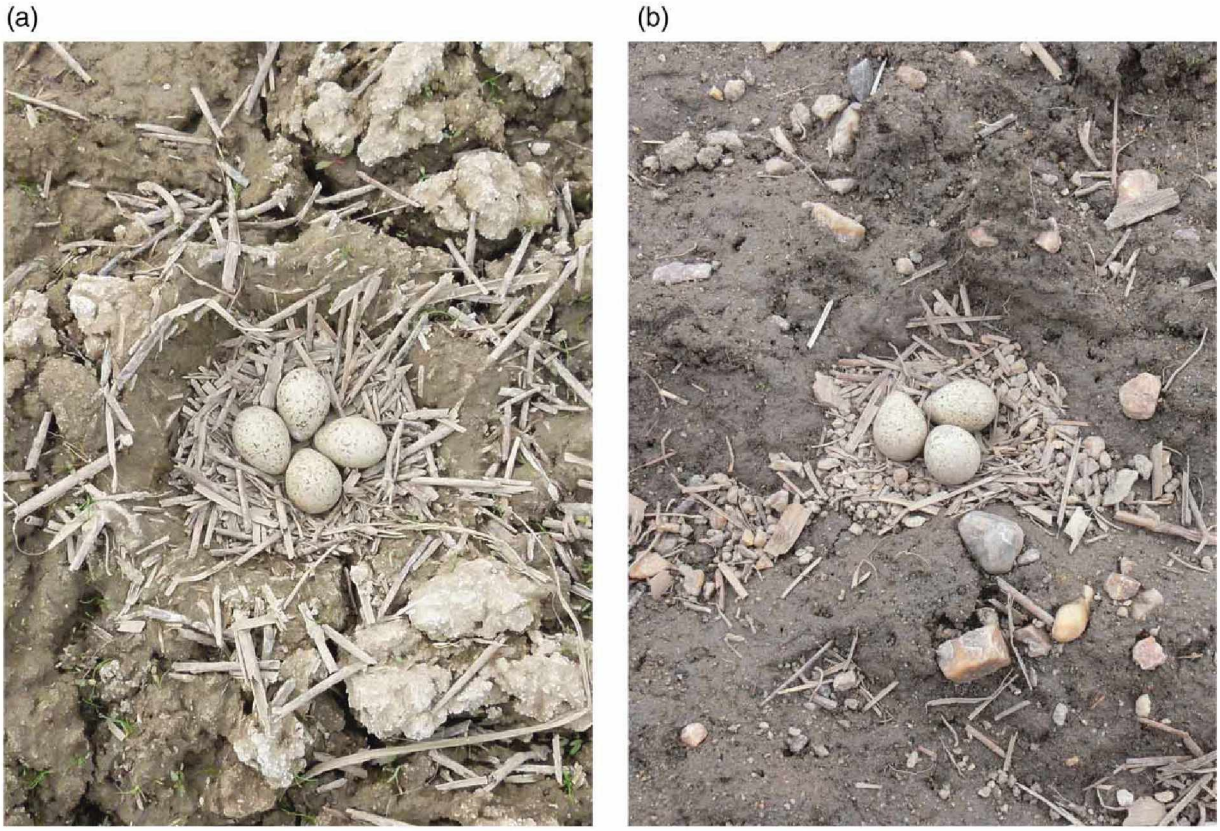

Figure 1. (a) Clutch of a Little Ringed Plover *C. dubius* in a nest scrape excavated by a Northern Lapwing *V. vanellus*, 27 May 2013, photo by MŠ. (b) An example of a 'normal' Little Ringed Plover nest in a ploughed field 20 km from nest (a), 9 April 2010, photo by VK.

lapwing nests in the middle of one large field (35 ha) near Žabovřesky (GPS: 48°59′53″N, 14°20′47″E), which was a wet ploughed field at the time of courtship and at the early incubation stage of both species. The inner cup diameter of plover nests (5.5–6.5 cm, $n = 13$) is smaller than that of lapwings (7–16 cm, $n = 96$) in the Czech Republic (Hudec & Šťastný 2005). At the study site, the lapwing nest scrapes with plover eggs appeared similar to other unused lapwing nest scrapes in the surroundings. One nest scrape (inner cup diameter: 12 cm, cup depth: 3.5 cm) with plover eggs was sparsely lined with pieces of straw but without stones (Fig. 1a), which does not correspond to the usual plover nest scrape lining (Cramp 1983), repeatedly found in the arable fields of South Bohemia (own unpubl. data, Fig. 1b). All eight eggs from the two plover clutches (four and four eggs) hatched successfully.

The majority of previously known inter-specific nest scrape reuses occurred after breeding of the host wader species. However, in this case, the plovers probably used unused lapwing nest scrapes. Although we cannot completely exclude possible predation of the lapwing nests during the egg-laying period and their subsequent reuse by plovers, this is unlikely due to our regular visits of the locality. We did not observe any physical conflict between the two species at the breeding ground and lapwings seemed to tolerate plovers in their territories. We suppose (according to the timing of breeding) that the plovers chose one of the nest scrapes which were excavated by lapwings during their courtship but were later unused for egg-laying and thus were free for the plovers.

The advantage of nest scrape reuse could be to save energy, similar to the arguments to support nest reuse (Pearson 1974). Saved energy can be invested in more intense display and courtship to potential mates as in the Fan-tailed Warbler *Cisticola juncidis* (Ueda 1989) or can lead to earlier laying of replacement clutches as in the Eastern Kingbird *Tyrannus tyrannus* in North America (Cancellieri & Murphy 2013). The energy-saving hypothesis is supported by the fact that nest scrapes of Kentish Plovers *Charadrius alexandrinus* were reused more often by the same species in the situations

when excavating due to firm soil was apparently more demanding (Amat *et al.* 1999).

In the plover and in other waders, where the female chooses one of the nest scrapes present in the territory (Cramp 1983), the incorporation of an already made nest scrape in the territory could increase the attractiveness of a displaying male. Moreover, a bigger nest scrape could serve as a supernormal stimulus (Staddon 1975) and the female could consider the male displaying beside this bigger nest scrape as more attractive. A bigger nest scrape could therefore be preferred for breeding to smaller ones excavated by the plovers.

The nearby presence of breeding lapwings could be an important advantage of the lapwing nest scrape usage. Lapwings are known for their aggressiveness in expelling avian predators from the surroundings of their nests (Elliot 1985, Kis *et al.* 2000). Deterrence of predators is more efficient in bigger colonies (Berg 1996, Šálek & Šmilauer 2002) such as the aggregation at the study site. As in Nankinov (1978), plovers at the study site could principally have sought out this 'lapwing protective umbrella'. Frequent observations of courting plovers at other lapwing breeding sites nearby to the study area (own unpubl. data) suggest that the phenomenon could be more widespread. The hatching success of plovers in South Bohemia is higher in fields compared to bottoms of dried fishponds which are traditional breeding habitat there (Cepáková *et al.* 2007). The presence of lapwing breeding colonies could play a significant role in this because lapwing colonies are currently situated particularly on arable land (Kubelka *et al.* 2012).

Alternatively, the finding of a plover nest in a tractor wheel track in East Bohemia (V. Štorek, pers. comm.) suggests that plovers are able to make use of similar unusual situations. It is therefore possible that plovers use any suitable depressions for their nests. Moreover, the pre-laying period of lapwings in 2013 was prolonged due to frosts at the end of March. Lapwing males thus had more time to excavate nest scrapes and indeed, more nest scrapes were found in the surroundings of active lapwing nests than in other years (Kubelka & Šálek 2013). Therefore, this surplus of vacant lapwing nest scrapes in 2013 could also have significantly influenced plover nest site selection.

At least 24 cases of inter-specific nest scrape reuse have been documented so far in 22 wader species (17 wader species used a vacant nest scrape built by another species) and in the majority of these cases it has only been recorded once. Most of them come from the Arctic (Table 1), probably as a result of longer persistence of nest scrapes in the stable arctic environment (Gratto *et al.* 1985, Soloviev *et al.* 2001) and possibly the energy demands for excavating/creating a nest scrape in cold Arctic conditions render nest scrape reuse more convenient. It could, however, also be caused simply by the fact that wader communities are thoroughly investigated in the Arctic, where several species breed close to each other in the same habitat (Soloviev *et al.* 2001) rendering the community more prone to inter-specific nest scrape reuse and its observation more likely. Generally, the species that reuse nests of other species do not differ much in size from the host species (Table 1). In contrast, in the case of plovers and lapwings, this difference in size is unusually large.

We conclude that plovers used the option of breeding in vacant lapwing nest scrapes in a ploughed field for one or a combination of the following reasons: (1) vacant lapwing nest scrapes were used simply as available suitable depressions in plover territories unconnected to their excavation by lapwings and the surplus of vacant lapwing nest scrapes in 2013 could have played an important role in what we observed; (2) bigger lapwing nest scrapes acted as a supernormal stimulus, which attracted courting plovers; (3) plover males enhanced their attractiveness to potential mates by including additional vacant nest scrapes in their territory and (4) plovers were attracted to breed in the proximity of lapwings to benefit from their anti-predation behaviour. All of these suggestions represent clear hypotheses that can be tested by experiment with a larger sample size.

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Our Bajkal Lake study plot and the nest od Long-toed Stint (*Calidris subminuta*), Russia 2013

Chapter 7

Coping with nest predation risk in a species-rich bird community inhabiting a Siberian wetland

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Coping with nest predation risk in a species-rich bird community inhabiting a Siberian wetland

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Abstract. Birds protect their nests against predators in various ways. In addition to active defence, they can hide their nests or use the protection of other species breeding nearby that actively defend the nests. Studies evaluating these strategies simultaneously are rare, especially from areas unaltered by humans. Nest predation risks were studied in a wetland bird community at Lake Baikal, Russia. The community contained several species actively defending their nests, although most were "passive defenders". Such tactics as active defence, concealed nesting, neighbourhood nesting and coloniality were tested for their effects on predation risk. The main predators were birds, particularly carrion crows (*Corvus corone*). Analysis of 193 nests using multimodel inference based on Akaike's information criterion suggests the most successful tactic was active nest defence, although most birds applying this tactic build open (uncovered) nests. Passive defenders effectively reduced this risk by nest concealment and/or breeding near active defenders. Opposing patterns were found for active versus passive defenders near the most successful breeder but also a potential nest predator, the Mongolian gull (*Larus mongolicus*). Conservation implications emphasize support for large aggregations of active nest defenders, vegetation cover providing good nest shelter, and sufficient area of interior habitat reducing edge effects.

Key words: anti-predator behaviour, breeding success, colonial breeding, Lake Baikal, nest concealment, protective umbrella hypothesis, waterbirds

Introduction

Nest predation is a key phenomenon determining breeding performance in birds (e.g. Skutch 1949, Lack 1966, Caro 2005, Lima 2009). Moreover, it is a major force in the evolution of avian life-history associated with such breeding traits as nest construction (Gill 2007), clutch size, number of brood, and caring for young (Martin 1995). Breeding birds have a significant capacity to assess and respond, over ecological time, to changes in the risk of predation to both themselves and their eggs or nestlings (Larsen & Grundetjern 1997, Albrecht & Klvaňa 2004, Caro 2005, Lima 2009, Dassow et al. 2012).

Various anti-predator behaviours of particular ground-nesting species have been found to reduce predation risk in individual bird species and under different circumstances. These include avoiding areas with high predation risk (Norrdahl & Korpimäki 1998, Tryjanowski et al. 2002), aggressiveness toward nest predators (Elliot 1985), placing nests in dense vegetation and thus enhancing nest concealment (Guyn & Clark 1997, Albrecht & Klvaňa 2004), clumping in colonies (Götmark & Andersson 1984, Šálek & Šmilauer 2002), and breeding in close proximity to "umbrella species" with active nest defence (Dwernychuk & Boag 1972a, Quinn & Ueta 2008).

Active nest defence against predators and nest concealment have been regarded as the essential adaptations of ground-nesting species to increase nesting safety in habitats threatened by predators (Lima 2009). In addition, various poor nest defenders as ducks (Dwernychuk & Boag 1972a, Götmark & Åhlund 1988), grebes (Burger & Gochfeld 1995), waders (Bub 1957, Nankinov 1978, Dyrcz et al. 1981, Larsen & Grundetjern 1997), and passerines (Eriksson & Götmark 1982) have been found to prefer breeding in close proximity to other birds, such as gulls, raptors and waders, which actively repel avian predators and thus provide reliable nest protection (reviewed by

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Quinn & Ueta 2008). These associations seemed to be particularly important in open habitats, such as tundra, wetlands and grasslands (Quinn & Ueta 2008). Surprisingly, it is not uncommon for such umbrella species as gulls also to be predators of other nests in the colonies (Dwernychuk & Boag 1972a, Larsen & Grundetjern 1997, Götmark 1989). Thus, decision making in these cases can be perceived as a trade-off between benefits gained from nest protection and costs ensuing from predation risk by protector species (Götmark 1989, Larsen & Grundetjern 1997, Quinn & Ueta 2008).

Nesting in large aggregations or in proximity to active nest defenders may be also accompanied by higher nest predation risk because some predators from a colony's surroundings can be attracted to areas with higher concentrations of nests. This phenomenon is described as the hypothesis of density dependent predation (Göransson et al. 1975, Andersson & Wiklund 1978, Larivière & Messier 1998). Andersson & Wiklund (1978) showed experimentally that such nesting in aggregations can be advantageous only if accompanied by active defence against predators. Without such defence, nesting is rather maladaptive and provides a clumped food resource to predators. Therefore, silent and cryptic nesting separately from other nests could potentially be beneficial for non-active nest defenders if predators preferably visit colonies in their area having limited abilities to defend themselves (e.g. small, loose colonies).

Different tactics are in use simultaneously and are easily studied worldwide within diverse bird communities inhabiting such open habitats as marshlands and tundra (e.g. Brunton 1997, Larsen & Grundetjern 1997, Götmark & Åhlund 1988, Caro 2005). Different species thus face various trade-offs in deciding upon how to optimize nest protection and reduce the risks of egg depredation. For example, nest crypsis is highly efficient for solitarily nesting mallards (*Anas platyrhynchos*) (Albrecht & Klvaňa 2004) while common eiders (*Somateria mollissima*) rely on nest attendance rather than on nest concealment (Bolduc et al. 2005). However, it is not clear how efficient are these tactics in diverse communities with colonies formed by active nest defenders potentially attractive for nest predators. Furthermore, there has been an absence of studies comparing anti-predator effectiveness of such tactics as nest concealment and active nest defence within the same areas. In particular, little is known about whether nest concealment of poor nest defenders with cryptic nesting (such as ducks or some shorebirds) is a more or less effective anti-predator tactic than nest defence of openly nesting active defenders (e.g. gulls, terns or lapwings). Moreover, numerous studies provide inconsistent results and interpretations as to whether the proximity of poor defenders to conspicuously breeding active nest defenders (whether or not they are potential nest predators) positively affects nesting success compared to separate nesting.

Although anti-predator tactics have evolved in natural communities, most recent studies are nevertheless based upon data collected in anthropogenic areas (e.g. Larivière & Messier 1998, Albrecht & Klvaňa 2004, but see Larsen & Grundetjern 1997) and thus come from human-altered communities (e.g. with impoverished habitat and species diversity, artificial densities of some introduced species, and/or modified structure and numbers of predators). Knowledge of predation risks in native communities is particularly important, however, for understanding those issues involved in communities modified by human activities within a cultural landscape, including managed wetland and grassland nature reserves.

The present study analysed nest success of birds within a diverse bird community in a native Siberian wetland at Lake Baikal, Russia. We tested 1) whether active nest defenders reduced probability of nest predation; 2) whether placing nests into dense vegetation (i.e. nest concealment) increased nest survival; 3) how

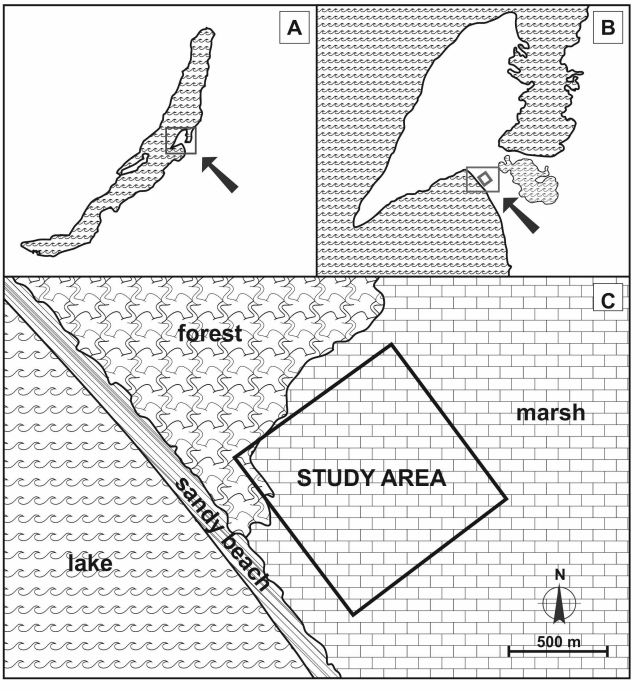

Fig. 1. Location of the study area on the isthmus of the Svjatoj Nos Peninsula, Lake Baikal, Russia. A) Lake Bajkal, B) Isthmus of the Svjatoy Nos Peninsula, C) Position towards the coast and forest.

clumping of aggressive nest defenders affect nest survival; 4) how efficient is using proximity to nests of aggressive defenders for successful breeding. The role of Mongolian gull (*Larus mongolicus*) which can be simultaneously a nest predator was particularly interesting in this context. Finally, we examined 5) whether nest predation is influenced by the proximity of the forest edge, from where a majority of predators penetrates. The effectiveness of anti-predator tactics was compared within the community, and it was investigated whether or when their combinations play a role. The study offers some recommendations for conservation management of species-rich avian communities inhabiting open wetlands.

Material and Methods

Study area

The research was conducted on the isthmus of the Svjatoj Nos Peninsula (Fig. 1), Lake Baikal, Russia, one of the key areas for wetland bird breeding in a wider region around Lake Baikal (Mlíkovský et al. 2002, Mlíkovský 2009). The isthmus of the Svjatoj Nos Peninsula, with an area of approximately 300 km², is covered mostly by a continuous mosaic of various open wetland habitats. The study area of approximately 1.4 km² is situated on the south-west edge of marshlands (53°33′ N, 108°56′ E) in order to include a gradient from the edge of a pine forest (taiga) to deep water with floating islands of vegetation. The habitats were formed by various plant associations (with diverse vegetation height of 5-50 cm) with dominant bog-bean (*Menyanthes trifoliata*) cover, sedges (*Carex* spp.) and mosses (for more details, see Mlíkovský & Stýblo 1992 and Šálek 2013). The taiga and shore of Lake Baikal near the study area provide excellent refuge for common generalist predators of bird nests, such as carrion crows (*Corvus corone*), ravens (*Corvus corax*) and red foxes (*Vulpes vulpes*) (see below).

Data collection

All fieldwork took place between 4 June and 12 July 2013. The basic study area of 1 × 1 km was subdivided into 12 bands (each with a width of about 85 m), recorded by GPS coordinates for easy location in the field. Three additional bands were subsequently added after primary inspection of the breeding grounds in the early season in order to take in more nesting attempts of various species within gull colonies, a typical phenomenon of the local wetland. All bands were surveyed carefully, repeatedly, and in random order by a team of 3-6 people to locate and measure bird nests. "Band trips" included slow walking with a span of up to 10 m between adjacent observers in shallower sections while inflatable boats were used to reach vegetation patches on deep water with floating islands. Nests were located by direct detection in vegetation or via parents indicating nest presence. All observers' movements were tracked using GPS devices. For all those nests found, including those already depredated or hatched, GPS positions were stored using waypoint averaging which facilitated recording the location with the highest possible accuracy (usually < 3 m). Species determination was made according to the presence of an adult bird, the colouration and size of eggs or eggshell remains, or, in the case of some duck species, feathers from the nest lining. Some of the nests remained unidentified (in particular, duck nests depredated in early incubation stages), and these nests were assigned to the corresponding genus (e.g. *Aythya* sp., *Anas* sp.). Prior to any manipulation at the nest, a photo of each nest was taken vertically from a height of 1 m to estimate nest concealment. While moving around the nest and manipulating the eggs, extreme care was taken to reduce handling time and impact on the surrounding vegetation in order to minimize predation risk caused by observers (Dwernychuk & Boag 1972a, b).

To assess the date of incubation start, the floating method was used (van Paassen et al. 1984, Mabee et al. 2006). The nests were checked after 10-15 days (during "band trips" or in separate inspections, if necessary) to determine nest fates. Nests were considered as successfully hatched when sufficient amounts of very small eggshell fragments were present in the nest cup linings (Green et al. 1987, Šálek & Šmilauer 2002, Mabee et al. 2006). The remaining nests, including those found with eggshell remains and those without any eggs before the expected hatching date, were considered as depredated.

To specify the anti-predation behaviour of each species, the behaviour of birds in the area was monitored and compared with findings from the literature. Based on 327 records of aggressive interactions between nesting birds and potential avian nest predators, five regular active nest defenders were identified: the common tern (*Sterna hirundo*) with 103 aggressive interactions, northern lapwing (*Vanellus vanellus*; n = 95), black-headed gull (*Chroicocephalus ridibundus*; n = 69), Eurasian curlew (*Numenius arquata*; n = 48), and Mongolian gull (n = 12). These species also repeatedly attacked approaching human observers. This list is in good agreement with previous findings from elsewhere (Cramp & Simmons 1983, Burger &

Gochfeld 1988, Montgomerie & Weatherhead 1988). The species most attacked were the carrion crow (n = 188 aggressive interactions) and Mongolian gull (n = 83), which should thus be considered as potentially important nest predators. To specify the range of real nest predators more thoroughly, photo-traps were installed in 20 artificial nests baited with hen eggs or with dummy lapwing eggs. The predators encountered were again mostly carrion crows and Mongolian gulls. In addition, the common gull (*Larus canus*) and red fox, the only mammalian predator, were detected.

Data analysis

For estimates of nest success, we applied the apparent method (Weidinger 2003). Thus, we scored each nest as successful, if at least one egg hatched, or unsuccessful, if the nest had been depredated before hatching. Given the team's intensive nest searching effort throughout the season, good visibility of open habitats, and conspicuousness of most nests, the success rate for finding nests was very high. Taking into account the incubation stage of all nests found as active (including those excluded from final analysis due to their abandonment or remaining active after completion of fieldwork), only 11 of 108 nests (10.2 %) with a known date of incubation start were shown to have been overlooked after one band trip while only four nests (3.7 %) so appeared after two trips. In addition, most of these nests had been overlooked at the laying stage when the parent birds were off the nests. Since it can be assumed that only a small number of nests were overlooked, we consider usage the apparent method instead of Mayfield method (Mayfield 1961) reasonable in this study (Weidinger 2003). Hence, the group of "successful" nests include also nests, which suffered partial egg loss. Although we suppose that partial predation may be widespread phenomenon in the study area (e.g. because carrion crows were observed carrying away individual gull eggs from gull colonies, own observations), we recorded only few direct evidences of partial predation (3 % of nests included into analysis). This did not allow us to provide a detailed analysis of predictors of partial predation. Nests which were abandoned before hatching or which were active (at least the first egg had been laid) even after completion of fieldwork were excluded from the analysis of their nest fates. Using the apparent method for estimates of nest success, it was possible to include into the analysis those nests found as inactive (n = 102, i.e. 52 % of all nests), without which the analysis would have been incomplete and possibly inappropriately biased.

Breeding species were sorted into three groups according to their anti-predator strategies (listed in Table 1). One group, called "active nest defenders", consisted of species which actively attack approaching nest predators but do not themselves threaten the nests of other species. These are the black-headed gull, common tern, Eurasian curlew and northern lapwing. The Mongolian gull was singled out in the specific category "potential nest predator", as it also depredates other nests. The last group, called "passive nest defenders", includes species which do not actively repel predators. These three distinct groups were analysed in separate models to reveal predictors that influence nest predation risk.

For each nest, the nearest active nest of an active nest defender and the nearest active nest of the Mongolian gull were included as two predictors of nest predation risk. In addition, the numbers of all active nests of both active and passive nest defenders (as a measure of nest density dependence) as well as the numbers of all active Mongolian gull nests (as a measure of the concentration of this specific nest predator) within a radius of 50 m were included as two additional possible predictors. The simplified rule with the arbitrary distance of 50 m was adopted based on previous experimental findings that at least some nest defending species, such as lapwings, respond to predators approaching at such a distance (e.g. Elliot 1985). In selecting the nearest nests and the nest numbers within a 50 m radius, only those nests were included which were considered active for at least one day during the expected lifetime of the nests for which the calculation was made (the "minimum one-day overlap" rule). The minimum one-day overlap rule was applied also to nests found inactive and for which the clutch's initiation date was unknown. In such cases, either the date of clutch initiation was approximated as the corresponding median date for other nests from the same species (synchronized gulls) or (for other species) egg laying was assumed to have started immediately after the last inspection of the site. In such cases, the expected lifetime of the nest was limited to one day.

Based on clearly detectable gradients across the marshland in moisture and distance from the beach as well as forest edge (Fig. 1), from which most potential nest predators can penetrate, inhomogeneous intensity of predation pressure was assumed in the study area. Based on this fact and given the relatively simple geometry of these gradients approximately corresponding to the cardinal points, the coordinates (latitude and longitude) of all nests were included as

transparent proxy predictors of nest predation risk to account for potential associated effects. Proportions of open water relative to other habitats in a network of squares 25 × 25 m across the study area was related to latitude (X) and longitude (Y) (Spearman rank correlation $r_s = 0.45$ and $r_s = -0.66$ for X and Y coordinates, respectively, both $P < 0.001$). Similarly, distance of nests to beach line was strongly related to the coordinates ($r_s = 0.53$ and $r_s = 0.61$ for X and Y, respectively, both $P < 0.001$) as well as distance of nests to forest edge did so ($r_s = 0.64$ and $r_s = -0.78$ for X and Y, respectively, both $P < 0.001$). All distance measurements were carried out using project layers in the ArcGis 10 (ESRI, CA, USA) environment.

Nest concealment was estimated as the proportion (%) of the nest construction hidden by vegetation when viewed from above. All estimates were done by a single investigator (MS) from a photo taken by an observer immediately after the nest had been found. However, due to overall vegetation growth, concealment of nests was significantly correlated with Julian date when the photo was taken ($r_s = 0.34$, $P < 0.001$). Thus, we additionally analyzed seasonal pattern in nest success using generalized linear model with binomial response variable (successful or depredated) (GLM_{binom}) on the subset of nests in which the date of incubation start was known.

To analyse probability of nest predation, the most parsimonious models were found using a multi-model inference approach based on Akaike's information criterion corrected for small sample size (AICc) (Burnham & Anderson 2002). The program R, version 3.1.1 (R Development Core Team 2014) with package MuMIn (Bartoń 2014) was used for computing the models. Two sets of generalized linear models for binomial distribution were computed, separately for active and passive defenders. In both cases, global models (GLM_{binom}) included all those predictors listed in Table 2. In total, 129 *a priori* models in each set were computed. The best candidate models were considered to be those with $\Delta AICc \leq 2$, but only those models which did not contain uninformative predictors were considered (Arnold 2010). To enable inference and ecological interpretation, even for those predictors not included into the most parsimonious models, for each of the included predictors cumulative Akaike's weights were additionally computed across the full model set as a measure of relative variable importance

Table 1. Species breeding in the area, predation risk strategy, number of nests found, mean (± SD) percentage nest cover.

Species	Strategy[a]	% in strategy	Number	Nest cover[b]	SD
Mongolian gull (*Larus mongolicus*)	1	100	44	3.1	0.88
Black-headed gull (*Chroicocephalus ridibundus*)	2	70	59	1.6	0.37
Common tern (*Sterna hirundo*)	2	13	11	5.0	1.44
Northern lapwing (*Vanellus vanellus*)	2	10	8	0.1	0.12
Eurasian curlew (*Numenius arquata*)	2	7	6	0.0	0.00
Unidentified duck	3	34	22	12.9	3.21
Tufted duck (*Aythya fuligula*)	3	26	17	35.3	5.71
Mallard (*Anas platyrhynchos*)	3	8	5	23.0	13.08
Red-necked grebe (*Podiceps grisegena*)	3	6	4	1.3	1.08
Wood sandpiper (*Tringa glareola*)	3	5	3	60.0	18.86
Pintail (*Anas acuta*)	3	3	2	0.0	0.00
Long-toed stint (*Calidris subminuta*)	3	3	2	35.0	10.61
Horned grebe (*Podiceps auritus*)	3	3	2	7.5	1.77
Ruff (*Philomachus pugnax*)	3	3	2	25.0	3.54
Shoveller (*Anas clypeata*)	3	1.5	1	50.0	0.00
Teal (*Anas crecca*)	3	1.5	1	10.0	0.00
Pochard (*Aythya ferina*)	3	1.5	1	10.0	0.00
Black-necked diver (*Gavia arctica*)	3	1.5	1	70.0	0.00
Unidentified grebe	3	1.5	1	20.0	0.00
Baillon's crake (*Porzana pusilla*)	3	1.5	1	100.0	0.00

[a] 1 = potential nest predator, 2 = active nest defender, 3 = passive nest defender. [b] Nest cover is expressed as percentage of the nest construction hidden by vegetation when viewed from above.

Table 2. Predictors included into the analysis of nest predation risk.

Acronym	Variable content
Xc	Longitude
Yc	Latitude
nNests	Number of nests of species other than Mongolian gull in a radius of up to 50 m
Distactive	Distance to the nearest nest of an active defender
nMong	Number of Mongolian gull nests in a radius of up to 50 m
Distmong	Distance to the nearest Mongolian gull nest
Concealment	Percentage of nest covered by vegetation, from vertical view

Table 3. The most parsimonious models (in bold) explaining nest predation risk for active and passive nest defenders.

Model	K[a]	AICc[b]	ΔAICc[c]	ω_i [d]	% explained variation
Active defenders					
Distmong[e] + Xc + Yc	**4**	**91.1**	**0**	**0.062**	**19.22**
Yc	**2**	**91.5**	**0.4**	**0.051**	**14.57**
nNests	2	93.5	2.36	0.019	12.65
Passive defenders					
Concealment + Distmong + nNests	**4**	**77.1**	**0**	**0.113**	**23.9**
Concealment + Distmong	**3**	**77.5**	**0.33**	**0.096**	**21.0**
Distactive + Concealment + Yc	4	80.5	3.41	0.021	20.1

[a] Total number of estimated regression parameters, including intercept. [b] Akaike's information criterion adjusted for small sample sizes. [c] Difference in AICc relative to the top model. [d] Akaike weight. [e] Predictors are defined in Table 2.

($\sum\omega_i$) (e.g. Marchetti et al. 2004, Tipton et al. 2008). This can be particularly important (Arnold 2010) inasmuch as some predictors were intercorrelated.

For mutual comparisons of the mortality rates among strategies, Tukey's multiple comparisons test was computed using the package multcomp in R (Hothorn et al. 2014). Because only 1 of the 44 Mongolian gull nests was depredated, the tactic represented by the Mongolian gull was used only for comparison of predation rates among the three anti-predator strategies and subsequent analysis was conducted only for active and passive defenders.

Results

Structure of the community

The analysed dataset consisted of 193 nests from 20 bird taxa including 18 identified species (Table 1). A major part of the community (59 nests, 30.6 % of all nests) was composed of the active nest defender the black-headed gull, followed by the potential nest predator Mongolian gull (44 nests, 22.8 %). Among active nest defenders, there were three other less abundant species, namely the common tern, northern lapwing and Eurasian curlew (25 nests, 13.0 %). Passive defenders made up a more diverse part of the bird community (14 species in total) and were dominated by ducks. The tufted duck (*Aythya fuligula*) was the most common passive defender (17 nests, 8.8 %), followed by the remaining identified ducks: mallards, pintails (*Anas acuta*), shovellers (*Anas clypeata*), teals (*Anas crecca*) and pochards (*Aythya ferina*) in total of 11 nests (5.7 %). Twenty-one duck nests remained unidentified (10.9 %). The other eight species categorized as passive nest defenders had 1-4 nests (8.3 % in total). Within the sum of nests, the proportions of passive nest defenders, active nest defenders (other than Mongolian gull) and the potential nest predator Mongolian gull, respectively, came to 33.7 %, 43.5 % and 22.8 %.

Nest predation rates and the most parsimonious models

We recorded 57 depredation events (29.5 % of all nests). The Mongolian gull potential nest predators were most successful in terms of nest survival probability, as only one of 44 monitored nests (2.3 %) was depredated. With 25 depredated nests (29.8 % of 84 nests), active nest defenders suffered from higher nest predation compared to Mongolian gulls (the difference being marginally non-significant, Tukey's

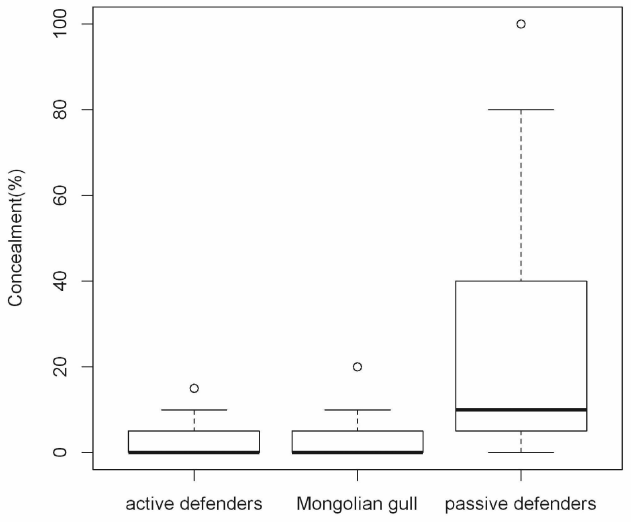

Fig. 2. Variation in nest concealment for three breeding strategies in a community of birds at the Svjatoy Nos marshland in 2013. Dark line: median, boxes: lower and upper quartiles, whiskers: 10 % and 90 % quantiles, circles: outliers.

test; $P = 0.053$). Among passive nest defenders, almost one-half of nests failed due to predation (31 nests, i.e. 47.7 % of 65 nests). This was significantly higher than for either Mongolian gulls or active nest defenders (Tukey's test; $P < 0.001$ and $P = 0.009$, respectively).

The most parsimonious models explaining nest predation risk for active and passive nest defenders were selected; for each of the two strategies, two models achieved $\Delta AICc < 2$ (Table 3). As shown, the strategies markedly differed in the most important predictors which appeared in the models. As only a single Mongolian gull nest was depredated, it would be pointless to analyse the effects of predictors responsible for nest predation risk in this strategy.

Table 4. Relative importance of predictors, expressed by sums of weights.

	Strategy[a]	
Predictor[b]	Active[c]	Passive[c]
Distmong	0.47	0.87
Concealment	0.43	0.97
nNests	0.40	0.48
Distactive	0.28	0.32
Yc	0.87	0.32
nMong	0.34	0.25
Xc	0.5	0.37

[a] Relative importance values indicate cumulative Akaike's weights ($\sum \omega_i$). [b] Predictors are defined in Table 2. [c] Strategy 1 = passive defenders; strategy 2 = active defenders.

The most parsimonious model for active nest defenders included both coordinates and distance to the nearest Mongolian gull nest (Table 3). In this model, latitude ($P = 0.001$, estimate = –675.5, SE = 207.9), and longitude ($P = 0.042$, estimate = 274.2, SE = 134.90) significantly contributed to explaining nest predation risk, thereby indicating lower predation risk further from the edge of marshlands. The third variable in the best model, distance to the nearest Mongolian gull nest, remained marginally non-significant ($P = 0.052$, estimate = 0.006, SE = 0.0032) and with a negative trend (i.e. increased predation risk near the nests). The second candidate model contains only one predictor: latitude ($P < 0.001$, estimate = –302.27, SE = 85.36).

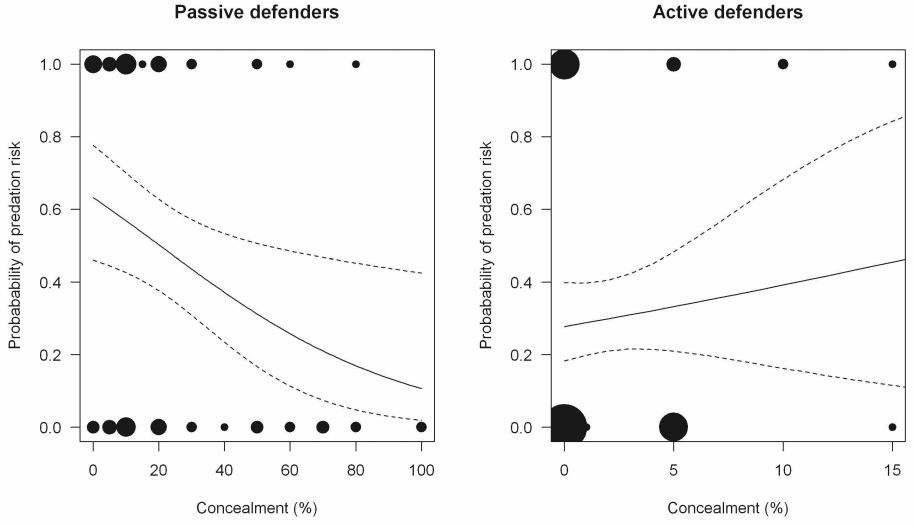

Fig. 3. Predicted probability of nest predation based on logistic regression with binary dependent variable (successfully hatched *vs.* depredated) for passive and active nest defenders in relation to nest concealment in the community of birds at the Svjatoy Nos marshland in 2013. Size of data points reflects sample sizes at each concealment category (from 1 to 41). Dashed line indicates 95 % confidence interval.

For passive nest defenders, the most parsimonious model (Table 3) included positive effects of nest concealment ($P < 0.001$, estimate = 0.039, SE = 0.0140), distance to the nearest Mongolian gull nest ($P = 0.012$, estimate = –0.004, SE = 0.0015), and a non-significant positive effect from the number of neighbouring nests ($P = 0.160$, estimate = 0.042, SE = 0.030). The second candidate model included only positive effects of nest concealment and the distance to the nearest Mongolian gull nest (both $P < 0.001$).

Predictors of nest predation

Nest concealment broadly differed between passive nest defenders and the two remaining strategies (Fig. 2). Passive defenders ranged broadly (between 0 % and 100 %) in the extents to which they concealed their nests (median 10 % of nest cover), and this had a strong effect on probability of nest survival ($\sum\omega_i = 0.97$, Fig. 3). In contrast, most nests of active nest defenders were entirely unconcealed (range 0-15 %, median = 0 % of nest cover) and the importance of this predictor for nest success among active defenders was markedly lower ($\sum\omega_i = 0.43$). Although this is a statistically non-significant finding, the trend toward surprisingly lower probability of nest survival with higher nest concealment is nevertheless worthy of note.

Because nest concealment significantly arised within season ($r_s = 0.34$, $P < 0.001$), we separately modeled overall seasonal pattern of nest success, indicating possible seasonal trends in predation pressure. Whereas the fixed effects of nesting strategy (active versus passive nest defense) and timing of clutch initiation were non-significant (GLM_{binom}: both $\chi^2 < 1.4$ and $P > 0.24$), the interaction of nesting strategy and timing of clutch initiation was highly significant ($\chi^2 = 7.7$, $P < 0.001$). This refers to opposite seasonal trends in predation rates in passive and active nest defenders; in active defenders the probability of nest survival during the season significantly decreased (estimate = –0.09, SE = 0.036, $P = 0.005$) while in passive nest defenders non-significantly increased (estimate = 0.036, SE = 0.031, $P = 0.250$).

Neighbourhood with nests of the Mongolian gull, a potential nest predator, showed effects for both active and passive nest defenders. For both strategies, the distance to the nearest Mongolian gull nest ("Distmong" in Table 4) was more important than was the number of Mongolian gull nests within a radius of up to 50 meters ("nMong", this predictor did not appear in any of the best models). However, the importance of the distance to the nearest Mongolian gull nest was much lower for active nest defenders than for passive defenders ($\sum\omega_i = 0.47$ versus 0.87, respectively).

Neighbourhood with other species

The cumulative weights of the two predictors representing this attribute, i.e. the number of all nests within a radius of up to 50 m and the distance to the nearest nest of an active nest defender ("nNests" and "Distactive", respectively, in Table 4), showed patterns clearly opposite those indicated by analogous predictors based exclusively on Mongolian gull nests. These predictors did not appear in the best candidate models, however, thus indicating their notably lower importance. The number of nests within a radius of up to 50 m was found to be more important ($\sum\omega_i = 0.40$ for active and 0.48 for passive defenders) than the distance to the nearest nest of an active nest defender ($\sum\omega_i = 0.28$ for active and 0.32 for passive defenders). Moreover, the effects of both predictors seemed to be positive (even though not very strong) for active as well as passive defenders.

Coordinates

Latitude (Yc) was the strongest predictor of nest success in the group of active defenders ($\sum\omega_i = 0.87$), for which longitude (Xc) also was of considerable importance ($\sum\omega_i = 0.50$). Neither of the coordinates seemed to be highly important, however, for passive defenders ($\sum\omega_i = 0.32$ for Yc, $\sum\omega_i = 0.37$ for Xc).

Discussion

Significant differences in probability of nest survival were found among the three anti-predator strategies of marshland birds. The nests of Mongolian gulls, which displayed one strategy, survived better than did the nests of the other birds pursuing the two remaining strategies (active nest defenders and passive nest defenders), thus indicating that "being a great gull" was definitely the most advantageous nesting strategy in the area. It is probable that active nest defence combined with large body size and colonial breeding led to successful intimidation of a wide range of potential nest predators including birds and mammals. Nests of active defenders had generally lower probability of nest predation than did those of passive defenders. This suggests that active nest defence can itself be a very effective anti-predator strategy. However, the effectiveness of individual anti-predator tactics practiced by active and passive defenders strongly differed. In particular, nest concealment itself as well as its influence on nest predation risk greatly

differed between these two strategies. First, whereas the nests of active defenders remained generally unconcealed and with only modest variation, the nests of passive defenders showed notably high variation in concealment. This difference probably resulted in the finding of no obvious effect of nest concealment for active defenders while concealment played a particularly important role in reducing nest predation among passive defenders. In the literature, we can find results both supporting (e.g. Dwernychuk & Boag 1972b, Brouwer & Spaans 1994, Guyn & Clark 1997, Traylor et al. 2004, Albrecht & Klvaňa 2004) and refuting (e.g. Crabtree et al. 1989, Colwell 1992, Vickery et al. 1992, Grant et al. 1999, Yerkes 2000, Thyen & Exo 2005, MacDonald & Bolton 2008a) the idea that there should be a positive effect of nest concealment on probability of nest survival in ground-nesting birds. In contrast to the results presented here, some studies regarding such passive nest defenders as ducks (Yerkes 2000) and Wilson's phalarope (*Phalaropus tricolor*) (Colwell 1992) found no support for the effect of nest concealment on nest survival or found a positive effect in an active nest defender (the herring gull *Larus argentatus*; Brouwer & Spaans 1994).

A probable explanation for these ambiguous results regarding the effect of nest concealment may consist in the different structures of predator communities among those areas studied (MacDonald & Bolton 2008a). Nest concealment can be particularly important where visually orientated avian predators play a key role (Brouwer & Spaans 1994, Traylor et al. 2004). If mammalian predators with olfactory orientation prevail, however, nest concealment is of much less or no importance (Crabtree et al. 1989, Vickery et al. 1992). Moreover, Crabtree et al. (1989) showed that for areas with strong mammalian predation pressure only the visibility of nests as viewed from the ground has a negative effect on nest success (as opposed to visibility from 30°, 60° and 90° above the ground). Our additional results in the forms of direct observations, pictures taken by photo-traps, and collected remains of depredated eggs or adults (the authors' unpublished data) suggest that the carrion crow and possibly also Mongolian gull (discussed below) were the dominant nest predators within the study area. The red fox, which also was confirmed to be a nest predator within the studied area, probably sought food mostly near the forest edge. An analysis of food remains at one fox den located next to the study area over two years (2013 and 2014) showed that the prevalent foraging habitats for foxes were forests and marshland edges. For example, the mallard, which regularly nests at the transition between forest and marshlands, was the only duck species determined in the food remains (the authors' unpublished data).

Because nest concealment significantly increased during the breeding season, it is also important to discuss whether the clutches initiated later in the season could not be less prone to predation for other reason than just nest concealment. For example abundance of other food resources for predators later in the season may reduce predation pressure on nests (Pienkowski 1984, Dinsmore et al. 2002, MacDonald & Bolton 2008b). However, as we found, seasonal increase in probability of nest predation in active nests defenders (which do not conceal their nests) is in contradiction with this assumption suggesting that the opposite trend for passive nest defenders (preferably masking their nests in vegetation) toward reduced nest predation risk is very probably associated with seasonal increase of vegetation cover.

Proximity to a Mongolian gull nest reduced probability of nest survival of active nest defenders, such as black-headed gulls and common terns. A clearly different and contrasting pattern was detected for passive nest defenders, such as ducks, for which proximity to Mongolian gull nests was one of the positive predictors explaining nest success. It can be supposed that whereas ducks are cryptic while incubating and thoroughly cover their eggs during incubation recesses (Kreisinger & Albrecht 2008), the nests of active defenders remained almost permanently visible and thus both Mongolian gulls and other predators required much less effort to find and depredate their eggs. It can be supposed, therefore, that Mongolian gulls did not actively seek duck nests and also that such intruding predators as carrion crows, which regularly prospected colonies of black-headed gulls and common terns and then took away captured eggs (own observations), had limited time to find and depredate hidden nests. That would be particularly true when the intruders were under attack by Mongolian gulls defending their own territories. Although there is no direct evidence that the Mongolian gulls also depredated the real nests at the study site, these gulls were recorded intensively robbing eggs from unprotected nests of startled great cormorants (*Phalacrocorax carbo*) near the study site on islands in the Čivyrkujskij Bay (the authors' unpublished data). Mongolian gulls were therefore probably able easily to overcome the defences of other active defenders nearby and fortuitously to capture eggs from their conspicuous nests (Verbeek 1988).

Only weak support was obtained for the effect of nest density on nest predation risk. For example, the distance to the nearest Mongolian gull nest was more important than the number of Mongolian gull nests within a radius of up to 50 meters (as an indicator of nest density). Admittedly, the number of all nests in a radius of up to 50 m was found to be more important than the distance to the nearest nest of an active nest defender, but the relative importance of both variables was rather small. Moreover, the number of surrounding nests was found to be a good predictor of nest survival probability in the best model only for passive defenders, although its effect was statistically non-significant. Opposing trends probably influenced this ambiguous result. Although on the one hand better protection within larger and/or denser nesting colonies can be expected (Götmark & Andersson 1984, Elliot 1985), on the other hand these colonies may attract more predators (Andersson & Wiklund 1978, Larivière & Messier 1998). Moreover, the active defence of smaller species such as the black-headed gull and northern lapwing may be sufficiently effective only when sufficient number of individuals cooperate (Elliot 1985). Those colonies appearing in the area during 2013 were rather small and sparse, and so these might not have provided adequate anti-predator protection.

Coordinates, and especially latitude, contributed significantly to explaining the variation in nest predation risk for active nest defenders. However, latitude was strongly correlated with distance from the marshland edge, which is itself also associated with water depth (increasing depth from the edge to marshland interior). This might suggest that predators (in particular terrestrial mammals) penetrating into the swamp from adjacent forests very easily reached nests situated closer to marshland edges. The risks arising from this possible edge effect (Skórka et al. 2014) points up the importance of size in designing protected areas to effectively support breeding species inhabiting internal habitats such as open wetlands (Arnold et al. 2007). To some extent, however, the latitudinal effect may be locally conditioned, as it was associated with the positions of large colonies of gulls, situated more to the south within the study site, and predation risk might therefore be lower there than in more northern sections with generally lower numbers of active nest defenders.

It is evident that the presence of the most successful nesting species, the Mongolian gull, significantly affected the results obtained in this study. We note that its population had steeply increased during the previous 20 years within the studied wetland. This was in contrast to the negative population trends for the majority of other breeding bird species (compare with Šálek 2013). The impact of great gulls on populations of other waterfowl has been broadly studied across the world. In many studies, great gulls have been detected as key nest predators (e.g. Götmark & Åhlund 1988, Vidal et al. 1998). On the other hand, protection from other predators has also been described (Dwernychuk & Boag 1972a). The impact of such great gulls as the Mongolian gull on the rest of the breeding bird community is certainly more complex than is seen solely in nest predation risk. It includes also competition for nest sites (Skórka et al. 2014), alterations in nesting habitat due to changes in plant composition around nests (reviewed by Vidal et al. 1998), and perhaps also higher predation pressure on hatchlings than on eggs (e.g. Dwernychuk & Boag 1972a, Chytil & Macháček 2000, Bowman et al. 2004). Therefore, Skórka et al. (2014) suggest that expansions of great gulls can have cascading and multilevel effects on populations of native species and may strongly alter the structure of the original communities. In any case, "great gulls" play an active role in shaping interspecific relationships, predation patterns, and population dynamics within wetland bird communities.

Finally, because of very intensive and long-lasting fieldwork, we cannot exclude that our results are influenced by our presence in the study plot. For example, in spite of our effort not to damage vegetation around the nests, we probably left some nests more conspicuous for predators than they had been before our visit (Dwernychuk & Boag 1972a, b). Some nests could also be betrayed to predators when incubating birds were flushed by observers (Götmark 1992). On the other hand, presence of observers in the study plot can also have a short-term positive effect, because of deterring predators directly by the observer themselves (Weidinger 2008). However, considering that our field effort covered whole study plot uniformly and intervals of visits were sparse, we believe that our influence of nest success was of minor importance and did not substantially affect the results (Götmark 1992).

In conclusion, this study reveals interspecific interactions among breeding birds within a diverse bird community inhabiting Siberian marshland is characterized by negligible anthropogenic impact and a natural structure of nest predator guilds. It demonstrates that a community consisting of a small number of actively nest-defending species together with a diverse group of passive defenders is characterized

by several complementary anti-predator tactics. In general, active nest defenders had higher chances of hatching offspring than did passive defenders. Active nest defence combined with the large body size of the Mongolian gull were two attributes resulting in the highest probability of nest survival for this species. Whereas passive defenders effectively reduced nest predation risk by nest concealment and by nesting in the proximity of active defenders, particularly the Mongolian gull, nest predation risk for birds applying active nest defence seemed to be less flexible and determined by predator incidence. As these active nest defenders built more conspicuous nests, they could increase nesting success by placing their nests farther from the forest edge and from the nests of Mongolian gulls. In any case, active nest defence itself remains the main factor positively influencing nesting success in the bird community. From a nature conservation perspective, it is particularly important to protect large colonies of active nest defenders, such as terns or smaller gulls, which may provide active protection for nests of the most passive defenders such as ducks or waders. It is essential, moreover, to maintain proper vegetation cover which may provide safe shelter for nests of passive defenders. Finally, conservationists should consider that a sufficient area of interior wetland habitats might reduce edge effects associated with increased predation risk.

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Bajkal lake marshland habitat with Bogbean and Marsh Sandpiper (*Tringa stagnatilis*), Russia 2014

Chapter 8

Beyond habitat: spatial structure of nesting wetland bird community is determined by conspecific and heterospecific attraction

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Beyond habitat: spatial structure of nesting wetland bird community is determined by conspecific and heterospecific attraction

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Direct habitat choice is considered the main mechanism way of nest site selection in birds. Much less attention has been devoted to other aspects of nest site selection, namely the demands for proximity to individuals of same or other species which can provide e.g., active protection against nest predators. All these aspects may become important for understanding the factors driving the spatial arrangement of nests in diversified (e.g., wetland) communities. This study aims to disentangle the contributions of habitat, conspecific attraction and heterospecific umbrella effects in nest spatial distribution of birds in a Siberian wetland, Russia, during seasons 1993 and 2013. In 1993 we included 25 identified species with 665 confirmed or probable nests while in 2013 there were 19 species with 188 nests. In both seasons, the nests were highly aggregated, due to all the effects of habitat, conspecific as well as heterospecific attraction. Active nest defenders like gulls and terns strongly attracted many other species representing cryptic breeders, particularly in 2013, probably as a result of increasing fear of predation risk within a generally impoverished community. We suggest that the spatial nest pattern within a bird community is modified by the natural dynamics of one or a few bird species even in relatively stable habitat. We emphasize that to comprehensively understand the nest site choice in species-rich bird communities such as in wetlands, both heterospecific and interspecific interactions should be considered. In areas where cryptic breeders are looking for neighborhood of active defenders, a support of abundant species with protective umbrella effect should be an important conservation measure.

Key words: anti-predatory strategies, Baikal Lake, breeding habitat, nest predation, nest site selection, Siberia, wetland birds.

INTRODUCTION

Bird parents actively choose suitable nest sites with the aim to avoid nest loss due to predation and harsh weather (Lloyd *et al.* 2000, Caro 2005). As a direct habitat choice has been considered the main way of nest site selection, most studies dealing with species distribution and numbers put the interpretation of their results within a framework of present or absent habitats (e.g., Sutherland & Hill 1995, Davis 2005, Baschuk *et al.* 2012, Zmihorski *et al.* 2016). However, individuals of numerous species may select the nest sites using a presence or absence of other animals instead of habitat (Caro 2005, Sebastián-González *et al.* 2010a,b). Aggregated conspecific nesting may comprise mutual awareness about food resources (*sensu* Bayer's 1982 study about colonies as information centres) or predator avoidance as such nesting may reduce relative individual risk (Larsen & Grundetjern 1997, Larsen & Moldsvor 1992). Additional benefit of shared nesting with other species actively defending their nests (Cramp & Simmons 1983) arises from creating a protective umbrella against potential predators, leading to higher nest survival in these associations (Larsen & Grundetjern 1997, Šálek & Šmilauer 2002, Sládeček *et al.* 2014).

Considerations concerning drivers of nest site choice become particularly important in large nesting aggregations of diverse communities where various interactions may overlap and interact, resulting in shared nesting. However, most studies refer to the inter-relationships for the spatial arrangement of bird communities on a level of two-(or few of) species (e.g., Eriksson & Götmark 1982, Burger 1984, Larsen & Moldsvor 1992, MacDonald & Bolton 2008, Bentzen *et al.* 2009, Kubelka *et al.* 2014, Cunningham *et al.* 2016). As far as we know, no study has attempted to quantitatively separate the effects of intraspecific and interspecific interactions from a pure effect of habitat selection within a diverse bird community.

Comprehensive studies of nest spatial patterns that analyse effects of different drivers using methods of variation partitioning are rare, although this approach has been found useful at coarser landscape scales (Drapeau *et al.* 2000, Hobson *et al.* 2000, Titeux *et al.* 2004, Boone & Krohn 2000, McIntire & Fajardo 2009). So far it has been applied in less species-rich bird communites inhabiting boreal forests (Heikkinen *et al.* 2004) and farmland (Freemark & Kirk 2001). In contrast, communities of wetland birds are highly diversified in terms of species habitat requirements (Paracuellos 2006, Żmihorski *et al.* 2016) and use of different anti-predator tactics (Gochfeld 1984, Sládeček *et al.* 2014, Cunningham *et al.* 2016) so that the motives for choice of nest sites can go far beyond the availability of preferred habitats in this environment. Distinguishing the motives can be then extremely important e.g. from conservation perspective, as the declines of some wetland species might likely be due to other reasons than the decline or alteration of their preferred habitats. The causes can lie in the loss of umbrella species which provide antipredatory defence or, on the contrary, in the emergence of new settlers acting as potential nest predators. Therefore, the knowledge of these effects revealed using proper statistical techniques can increase the value of observational studies (McIntire & Fajardo 2009) in terms of conservation implications (Dray *et al.* 2012). For example, we might be interested whether species impoverishment of a community may lead to a greater focus of the remaining species on nest site selection based on the habitat, or to higher aggregation, aiming to asserting the anti-predator umbrella. In this

case, the umbrella species may play even the role of keystone species in the community (Boogert *et al.* 2006).

This study analyses spatial arrangement of nests within a bird community inhabiting a large natural wetland during two breeding seasons separated by a twenty-year period. Our prior aim was to assess the role of intra- and interspecific interactions beyond the effects of mere habitat preferences. First, we tested whether the effect of clumping adds beyond the explained variation in spatial distribution of breeding birds given by the habitat in active nest defenders, which tend to nest colonially. Second, we find out how far the cryptic breeders are prone to share heterospecific nesting with active defenders. In addition, we discuss the result in the light of differences between the two years with different structure of the bird community.

METHODS

Study Site

The research was conducted on the isthmus of the Svjatoj Nos Peninsula, Lake Baikal, Russia (Supporting Online Information S1A,B). The isthmus of an area of approximately 300 km² is covered mostly by a mosaic of open wetland habitats and is one of the key areas for wetland birds breeding in a wider region around Lake Baikal (Mlíkovský *et al.* 2002, Mlíkovský 2009). The study area was situated in marshlands (53°33′ N, 108°56′ E) and included a gradient from the edge of a pine forest (taiga) to deep water with floating islands of vegetation. The habitats are formed by various plant associations (with diverse vegetation height of 5-50 cm) dominated by bog-bean (*Menyanthes trifoliata*), sedges (*Carex* spp.), and mosses (for more details, see Sládeček *et al.* 2014). The taiga and shore of Lake Baikal near the study area provide refuge for generalist predators of bird nests, such as carrion crows (*Corvus corone*), ravens (*Corvus corax*) and red foxes (*Vulpes vulpes*) (Sládeček *et al.* 2014).

Data Collection

All fieldwork took place in the breeding seasons between 4 June and 13 July in both 1993 and 2013 in the same study area of 1.64 km^2. In 1993, the area was sub-divided into 100 × 100 m squares outlined with color flags, and each square has been systematically explored by one-person (MŠ) twice to three times during the season. Fieldwork aimed in nest search and bird mapping and was carried out daily with slow walk or using inflatable boats along twisting lines throught the squares. The found nests were marked using color flags tied to vegetation 5 m away and their positions were recorded into field maps. Repeated observations of birds with territorial behavior were considered as probable breeding. In 2013, the area was subdivided into 15 bands (each with a width of about 85 m), recorded by GPS coordinates. All bands were surveyed repeatedly and in random order by a team of 3-6 people to locate and measure bird nests. The surveys included slow walking with a span of up to 10 m between adjacent observers in shallower sections while inflatable boats were used to reach vegetation patches on deep water with floating islands. All observers' movements and nest positions were tracked using GPS devices.

In both seasons, species determination of the nests usually was possible following incubating birds, but sometimes (in nests discreetly left unattended) we used colouration and size of eggs or eggshell remains, or, in the case of some duck species, feathers from the nest lining. Yet, some nests remained unidentified (in particular, duck nests depredated in early incubation stages), and these nests were assigned to the corresponding genus (*Aythya*, *Anas*, *Podiceps*). While moving around the nest and manipulating the eggs, extreme care was put to reduce handling time and impact on the surrounding vegetation in order to minimize predation risk. Incubation stage was measured in most nests using flotation test (van Paassen *et al.* 1984).

We distinguished four main habitat types (Supporting Online Information S2A,B): (1) Trees on transition between taiga and swamps [In Figures and Tables abbreviated as Wood]; (2) Diverse vegetation dominated by high (50-90 cm) sedges or bush-grass tufts somewhere with dwarf willows [DiversVeget]; (3) Moss dominated and up to 20 cm tall sparse vegetation cover on highly wet sites but lacking open water [Moss]; (4) Continuous open water somewhere with emergent plant cover and floating islands [Water]. Proportions of all four habitats were recorded within particular squares (Supporting Online Information S2C,D). In addition, we measured water depth in the centres of quadrats (in the field) and the nearest distance to marshland edge (using map).

Data Analysis

The area was divided into 164 squares 100 × 100 m with the same position in both years and each of them were used as a unit in analysis. For the purposes of this study we defined two bird groups (guilds) with distinct anti-predator defense tactics. The first group, active nest defenders, encompasses species that are willing to actively attack approaching predators and expel them away from nest territories (Caro 2005). They are thus able to protect the nests of their neighbors, including other species nesting nearby that do not possess aggressive behavior. The second group, called here as cryptic breeders, includes all remaining species that do not use aggressiveness as a major anti-predator tactic. Instead, they apply many different behavioral alternatives from discreet leaving the nest or remaining motionless and cryptic on it to performing conspicuous actions combining distraction display and scolding with (or without) simulation of injury before the predator approaches the nest (Caro 2005). The sorting of species into the two groups was performed using published knowledge (Cramp 1977, 1985, Larsen & Moldsvor 1992) and verified by own field observations. We compared the timing of breeding between active defenders and cryptic breeders using Kruskal-Wallis χ^2 test. Should active defenders influence nest site choice of cryptic breeders, they have to start nesting generally earlier.

As some duck and grebe nests found without incubating adult were difficult to reliably determine, we analysed all fowl ducks merged into one group *Anas* spp. except the Teal (*Anas crecca*) which is well distinguishable according to egg size (Cramp 1977). Both diving ducks (pochards *Aythya fuligula* and *A. ferina*) we merged into the group *Aythya* spp. and grebes into the *Podiceps* spp. group. All these merged groups comprise only cryptic breeders. Mongolian Gull (*Larus mongolicus*) was included as a separate category (and predictor in the models) due to its ambiguous nature (aggressive nest defender but also a potential nest

predator). As passerines are not associated directly with wetland habitats, we excluded them from analysis.

We distinguished three groups of predictors: (1) habitats, including percentage cover of the four habitat types, water depth and the centred quadrate' distance to the nearest edge (mainland with a firm ground); (2) descriptors of active nest defender species presence and abundance in predicting nest patterns of cryptic breeders; (3) spatial descriptors, representing a combination of spatial coordinates (latitude/longitude) and the spatial eigenvectors calculated using the distance-based Moran eigenvector maps (dbMEM) method. This method processes adjusted matrix of distances among sampling sites using principal coordinate analysis (PCoA), and creates in this way a set of predictors, able to describe variation at any spatial scale accounted for by the sampling design. Consequently, this full set of predictors must be reduced to a parsimonious subset using stepwise selection (see Legendre & Legendre 2012 for additional details). Although the spatial coordinates, which may represent only global trends across the study area, can be also represented by a combination of spatial eigenvectors of the dbMEM method, we followed the suggestion of Legendre & Legendre (2012, p. 868) to model the global trends separately and use them (if ascertained as significant predictors) as covariates when calculating the spatial eigenvectors. Together, the selected spatial coordinates and computed eigenvectors complement each other and form a group labelled as spatial predictors.

To analyse the spatial pattern of breeding birds (spatial autocorrelation among the quadrats) in 1993 and 2013, we calculated the Moran's *I* using the numbers of all nests across taxa in the squares (package *ape*, R version 3.2.2; R Core Team 2015). For habitats, correspondence analysis (CA) of data on proportions of four habitat types in every square was used, separately for each season, to summarize numerically the most important gradient in habitat composition – the first CA axis. Scores of individual squares on this axis (representing 67% and 73% of the total habitat variation in years 1993 and 2013, respectively) were then used to estimate spatial autocorrelation of habitats using Moran's *I*. We have also analysed (by CA) the data on proportions of particular habitats pooled across the two study seasons to compare the differences between the seasons in habitat availability (Supporting Online Information S2E).

We have evaluated the compositional variation in bird assemblages recorded within individual quadrates using redundancy analysis (RDA, Legendre & Legendre 2012), mostly in the form of partial RDA, including *a priori* covariates to separate effects of individual predictor groups (Supporting Online Information S3). Original nest counts were log(x+1)-transformed to stabilize the unexplained (residual) variation, and very rare species (occurring in just one or two squares) were excluded from the analyses. All analyses included also the squares without any nest. To separate the effects of various predictor groups, we have used the variation partitioning approach (see Legendre & Legendre 2012). As we tested for a hypothesized effect of active defenders on the group of cryptic breeders, we have performed the variation partitioning separately for each of these two groups, distinguishing just two groups of predictors for the community of active defenders, but adding the third group of predictors (representing the effect of active defenders) to the variation partitioning for the sub-community of cryptic breeders.

For each set of response data (active defenders vs. cryptic breeders, and 1993 vs. 2013 data), we have first chosen a minimum adequate subset of predictors in each group using stepwise selection. Because this method presents an inherent danger of overestimating the set of required predictors, we have applied measures limiting such a bias based on suggestions of Blanchet *et al.* (2008): (a) before selecting from a group of predictors, a permutation test of significance was performed using the whole group and if the joint effect was not significant ($P > 0.05$), no predictors were selected; (b) primary stopping criterion in the predictor selection was based on a partial permutation test (of the candidate predictor effect in addition to already selected predictors) and the estimated P-values were adjusted in the case of spatial predictors (where a large pool of candidate predictors substantially inflates Type I error) by transforming them into false discovery rate (FDR) estimates (Verhoeven *et al.* 2005); (c) an additional stopping criterion was based on calculating R^2_{adjusted} for a constrained ordination using the whole group of predictors, which served as a reference value. When this reference value was exceeded by R^2_{adjusted} of the selected predictor subset, the selection was stopped. As open water supplied reduced nesting opportunities for most species (e.g., on floating islands and plant deposits), we preferably selected the remaining variables, if they emerged among the significant candidate predictors.

When interpreting the results of variation partitioning using groups with different counts of selected predictors, it is important to take into account that the additive (and therefore partitionable) explained variation is generally expected to increase with the increasing number of predictors. We have therefore (a) used adjusted form of explained variation (corresponding to R^2_{adjusted} in linear regression) and (b) also interpreted mean square statistics, where the explained variation is divided by the number of model degrees of freedom. Note that such mean square values can be computed unequivocally only for the unique contributions of individual groups, not for the fractions representing overlap in explained variation.

All tests of hypotheses concerning multivariate data (in constrained ordination framework) were done in Canoco 5 software (ter Braak & Šmilauer 2012), using Monte Carlo permutation tests based on pseudo-F statistics, as their traditional more parametric counterparts are not available here (ter Braak & Šmilauer 2012, p. 72). Pseudo-F statistic values are presented with a simplified "F" label. As we are comparing just two sampling times separated by 20 years, we analyzed each sampling time separately rather than focusing on an (inefficient) interpretation of the time*predictors interaction terms in a dataset pooled across the two distant seasons. Also the community patterns were evaluated separately for both guilds, based on our *a priori* assumed hierarchical nature of their relationship, with both groups of species affected by spatial and environmental predictors, but cryptic breeder species further responding to the presence of active nest defenders. Because a significant effect of a predictor on community composition does not necessarily mean that all species are responsive to that predictor, we emphasize in ordination diagrams (where appropriate, i.e. for constrained ordinations with a single or few predictors) responsive taxa, based on the suggestions derived from t-value biplots (ter Braak & Šmilauer 2012, p. 226).

RESULTS

Community composition and spatial pattern of nests

In 1993, we identified 25 species with 665 confirmed or probable nests while in 2013 the numbers dropped to 19 species with 188 confirmed nests (Supporting Online Information S4A). From eight species of active nest defenders in 1993, only four with strongly reduced numbers remained in 2013. The most notable differences between the two seasons include disappearance of three previously common active defenders White-winged Black Tern (*Chlidonias leucopterus*), Little Gull (*Hydrocoleus minutus*) and Common Gull (*Larus canus*). In contrast, the Mongolian Gull was only active defender that newly settled to breed in the area. Also 17 species classified as cryptic breeders in 1993 decreased to 14 species in 2013, with paticular loss of previously sparse Asiatic Dowitcher (*Limnodromus semipalmatus*). The spatial pattern of nests across taxa was aggregated in both years (Supporting Online Information S4B). The Moran's I ($I_{1993} = 0.05$, $I_{2013} = 0.01$) were positive and significantly higher ($P < 0.05$) than expected for random pattern (with no spatial autocorrelation) in 1993 and 2013 [$I_{1993} = -0.006 \pm$(SD)0.0059 and $I_{2013} = -0.006 \pm$(SD)0.0034].

Active nest defenders started to breed significantly earlier than cryptic breeders in both years (1993: May 29 as a median day for 107 nests of active defenders and June 6 for 45 cryptic breeders, Kruskal-Wallis $\chi^2_1 = 12.6$, $P = 0.0004$; 2013: May 29 for 44 active defenders and June 15 for 63 nests of cryptic breeders, Kruskal-Wallis $\chi^2_2 = 44.2$, $P < 0.0001$).

Habitat structure

The most dominant habitat of the four distinguished categories in both years was moss followed by water, which, however, markedly changed from 1993 to 2013 (Supporting Online Information S2D). Whereas the proportion of moss remained relatively stable, open water decreased by 14% in average (median 6%) while diverse vegetation increased by 11% (median 0%). In addition, spatial distribution of particular habitats changed only moderately between 1993 and 2013 (Supporting Online Information S2E). Observed Moran's I for the scores of habitat ($I_{1993} = 0.19$, $I_{2013} = 0.32$) was significantly higher ($P < 0.05$) than expected for random pattern in both years [$I = -0.006 \pm$(SD)0.0071 for both years] suggesting aggregation of particular habitats throughout the area in both years.

Active nest defenders in 1993

We found a significant effect of latitude ($F = 12.4$, $P = 0.001$) explaining (R^2_{adjusted}) 7.5% of total variation in species composition and this effect was included among spatial predictors as a covariate. After removing the global latitudinal trend, habitat descriptors significantly contributed to spatial nest pattern of this group (test of significance on all canonical axes: $F = 3.9$, $P = 0.002$). Three habitat predictors were chosen based on their significant effects – diverse vegetatiton, moss and water depth (Table 1A). Active nest defenders avoided nest sites on deep water with a trend of some waders to prefer diverse vegetation and moss (Supporting Online Information S5A). However, unique contribution of habitat predictors to

the total explained variation was only <0.1%. A substantial part of their explanatory power was shared with the spatial predictors (7.7% of the total variation; Table 2A; Fig. 1).

In addition to latitudinal spatial gradient, there were other 28 significant spatial eigenvectors (test of significance on all canonical axes, $F = 9.4$, $P = 0.001$; Supporting Online Information S6A), which uniquely contributed with 51.6% of the total variation in community composition of active nest defenders in this year (Table 2A; Fig. 1). When comparing the mean square statistics for unique habitat and unique spatial predictor effects, the effect of space (per single predictor) was >8 times larger than the effect of habitat.

The spatial predictors played a similar role in nest patterns of three larids – Black-headed Gull (*Chroicocephalus ridibundus*), Little Gull and Common Tern (*Sterna hirundo*), while nest spatial pattern of White-winged Black Tern was different (Supporting Online Information S5B). Therefore, although the nest pattern of active nest defenders was significantly influenced by habitats, spatial patterns were prominent and little affected by habitat distribution.

Cryptic breeders in 1993

Variation partitioning with three groups of descriptors, representing habitats, neighborhood with active defenders and spatial predictors, showed that habitats contributed significantly to explaining the nest placement (test on all canonical axes: $F = 3.0$, $P = 0.0016$). Moss cover was the only significant predictor selected in forward selection procedure (Supporting Online Information S6B), suggesting mild preferences of this habitat by some waders as Common Snipe (*Gallinago gallinago*), Wood Sandpiper (*Tringa glareola*) and Ruff (*Calidris pugnax*) but avoidance by grebes (Supporting Online Information S5C). The active nest defenders contributed marginally significantly (test on all canonical axes: $F = 2.8$, $P = 0.033$) with a particular importance of their numbers (Table 3A) on occurrence namely of greebes and partly of *Aythya* ducks but not on most waders and *Anas* ducks (Fig. 2).

Among spatial predictors, beyond latitude, two other spatial eigenvectors (Supporting Online Information S6C) were chosen as significant (test on all canonical axes: $F = 1.5$, $P = 0.0002$) for their joint effect. Spatial predictors had a larger unique contribution (4.7%) to the total (adjusted) variation than active defenders (2.1%) and particularly than habitats (0.4%). Moreover, spatial predictors shared a large part of their explanatory power with habitats (4.8% of the explained variation as a sum of 'f' and 'g' fractions) but only a little with the effect of active defenders (0.5% as a sum of 'e' and 'g' fractions) (Table 4A; Fig. 1). Some species were similar in their spatial nesting patterns (occurrences) and differed in this respect from the others as seen from their response to the effects of selected spatial predictors. For example, occurrences of ducks (both *Anas* spp. and *Aythya* spp.) resembled in spatial gradient some waders as Common Snipe while differed from species as Wood Sandpiper, Marsh Sandpiper (*Tringa stagnatilis*), and particularly grebes (Supporting Online Information S5D). Overall, the average strength of active defender predictors and spatial predictors was more than two times greater than the strength of habitat predictors, as judged by the mean square statistics (Table 4A; Fig. 1).

Active nest defenders in 2013

The effect of latitude (F = 7.8, P = 0.001) was significant and explained 4.0% of the total variation in species data and this effect was therefore included in further analysis. After removing the global latitudinal trend, the analysis revealed that the nest site choice of active defenders was driven by habitats (test of significance on all canonical axes: F = 4.0, P = 0.009), in particular by moss and diverse vegetation (Table 1B) exclusively explaining 4.6% of the adjusted total variation in species data (Table 2B; Fig. 1). Appearance of non-colonial Eurasian Curlew (*Numenius arquata*) correlated with the amount of diverse vegetation while semicolonial Northern Lapwing (*Vanellus vanellus*) showed positive response to moss. Larids as Common Tern, Black-headed Gull and Mongolian Gull avoided both these habitats (Supporting Online Information S5E). However, another 3.7% of the total variation was explained jointly by the selected habitat descriptors and latitude (selected spatial predictor), suggesting considerable overlap of both explanatory components.

Among spatial predictors (Supporting Online Information S6A), only latitude significanly contributed to explaining spatial nest pattern of active nest defenders, with (adjusted) 0.3% of total variation in species data (Table 2B; Fig. 1) having thus negligible explanatory power compared with the effect of habitat. This is supported also with the mean square statistic, where the average strength of habitat predictors exceeds the selected spatial predictors more than three times.

Cryptic breeders in 2013

Latitude (with global test on all axes: F = 1.8, P = 0.0006) was chosen as the only significant representative spatial predictor. Variation partitioning with three groups of predictors revealed significant unique effects in two of them. The effect of habitats (test on all canonical axes: F = 4.6, P = 0.004) included moss and diverse vegetation as two significant predictors selected in forward selection procedure (Supporting Online Information S6B). In general, these habitats were preferred by some shorebirds but avoided by ducks and grebes (Supporting Online Information S5F). Three predictors describing the effects of active defenders (test on all axes: F = 34.8, P = 0.0002) – presence of nests of an active defender, nest count for active defenders, and presence of Mongolian gull nests – were selected as highly significant ones (Table 3B). Ducks and grebes, unlike waders, built their nests preferably besides the nests of active nest defenders, with the exception of Mongolian Gull (Fig. 3).

Similar to the response to active nest defenders, ducks and grebes differed from waders regarding the effect of space and all the spatial effects overlapped entirely with the habitat and active defender effects. Habitat predictors had a very small unique contribution (1.3% of total explained variation) compared with the unique effect of active defenders (32.4% of the total explained variation), as further evidenced by the mean square statistic for those unique effects (Table 4B; Fig. 1). Shared effects were important among all three groups of predictors, with the highest contribution by the overlap between all three groups together (3.7%).

DISCUSSION

Diverse habitat mosaic of extensive wetlands supports the formation of rich bird communities dominated by colonial species like gulls and terns, accompanied with other, less conspicuous species as ducks, shorebirds, grebes, divers, rallids etc (e.g., Baschuk *et al.* 2012, Pagel *et al.* 2014). We have demonstrated that all three considered groups of predictors – habitat type, neighborhood with other species, and additional spatial effects particularly attributable to intraspecific interactions – effectively contributed to nest spatial patterns within the community. Additionally, segregation of the community into two groups (guilds) – the active nest defenders and the cryptic breeders – provided a more detailed insight into the processes driving the spatial distribution of nesting birds. While species composition as well as nest spatial patterns strongly differed between the two years of study, habitat changes were small, comprising mostly a minor loss of water area in favor of diverse grassy sedges. This suggests that the changes in nest spatial patterns were rather due to changes in the community structure than in habitat structure and that the sole habitat predictors cannot provide exhaustive explanation of spatial nest patterns in these diverse communities with manifold intra- and inter-specific interactions.

Habitats, thought to be a 'first hand' set of predictors explaining species distribution, played a role in both guilds and both years. Detailed inspection revealed that shorebirds preferred diverse vegetation mosaic away from deep water but this has not been the case in larids, grebes and ducks. These findings fit with previous studies (e.g., Duebbert *et al.* 1983, Frederick & Collopy 1989). General avoidance of moss by most birds was probably associated with too low and uniform vegetation cover, which gave only little opportunity to conceal nests, thus enabling easy access for both avian and mammalian predators. Only the Northern Lapwing with cryptic eggs that prefers a good view from the nest (Cramp & Simmons 1983) and is active in repelling predators from the nest vicinity (Elliot 1985) perceived it as a suitable habitat for nesting.

A unique effect of space descriptors proved to explain much of bird nesting preferences far beyond the variability explained through the habitat, particularly in 1993. We suggest that most of this effect found in active defenders arose from their conspecific attraction resulting in colonial breeding (Rolland *et al.* 1998). These species behave conspicuously during incubation period (Cramp & Simmons 1983, del Hoyo *et al.* 1996) and easier detectability of their nests by predators directly or through incubating parents (except the Eurasian Curlew; own observations) needs to be compensated, e.g. by a shared protection (e.g., Gochfeld 1984, Šálek & Šmilauer 2002). The three common larids, Black-headed Gull, Little Gull and Common Tern shared habitat association as well as similar spacing in 1993, reflecting the fact they formed heterospecific aggregations. As we showed previously, they appeared preferably on islets above deep water away from marsh edges, which prevented the access of predators from adjacent forest (Sládeček *et al.* 2014). Although aggregating behavior was perspicuous in abundant gulls and terns, it was less obvious in uncommon active defenders like Eurasian Curlew or Northern Lapwing. On the contrary, these waders showed clear habitat preferences. One explanation is that their local populations were limited to a few pairs preventing them to create large colonies but enabling to occupy preferred habitats. Moreover, both these species combined their active defense with nest crypsis, either through

incubating parents as in the case of Eurasian Curlew (Nethersole-Thompson & Nethersole-Thompson 1986) or through camouflaged nests in the Northern Lapwing (Cramp & Simmons 1983, Šálek & Cepáková 2006), allowing them to safely inhabit more exposed habitats e.g. nearby marshland edges.

In addition to the revealed habitat preferences and aggregating behaviour of most active nest defenders, we have shown cryptic breeders as tending to share colonies with active defenders regardless of habitat. Such behavior was previously described for particular species, e.g. Bar-tailed Godwits (*Limosa lapponica*) with aggressive Whimbrels (*Numenius phaeopus*) (Larsen & Moldsvor 1992) or ducks (*Anas* sp. and *Aythya* sp.) with actively defending Black-headed Gulls and Little Gulls (*Hydrocoleus minutus*) (Vaananen *et al.* 2016). The species lacking a pronounced active nest defence may benefit from the protective umbrella against predators provided by actions of active nest defenders. This may result in generally higher nesting success, as has been described in Black-necked Grebes (*Podiceps nigricollis*) sharing colonies with Black-headed Gulls (Fiala 1991) or in White-tufted Grebe (*Rollandia rolland*) and Silvery Grebe (*Podiceps occipitalis*) within the colonies of Brown-hooded Gull (*Chroicocephaus maculipennis*) (Burger 1984). Our study extends these previous findings and shows that clumping of breeding birds represents a general rule for spatial nesting structure across the whole wetland bird community. In addition, we demonstrate that particularly the numbers of active nest defenders, not only their presence, attracted cryptic breeders such as grebes and ducks to settle nearby. We suggest that in such mixed colonies the advantage of cryptic breeders lies in lower nest predation risk even if the predators penetrate the colony because the active defenders build less concealed and thus easily detactable nests (Sládeček *et al.* 2014).

As spatial clumping of species differed between 1993 and 2013, we may expect its varying importance in same area according to circumstances within the actual community. In particular, the effect of active nest defenders as neighbors actively sought by cryptic breeders excelled as much stronger in 2013 than in 1993 probably because of dramatic impoverishment and dilution of the bird community in 2013. Especially a complete loss of the large population of colonially nesting White-winged Black Terns (with at least 297 confirmed or probable nests spread across the area in 1993, but completely missing in 2013) could dramatically affect the nest site choice of cryptic breeders. It was the most common active nest defender without apparent habitat preferences, able to breed on swampy standing water and transitional or fluctuating marginal inundations regardless of water depth (Cramp 1985). Baikal Lake lies at the northern edge of the species' patchy distribution in this part of Asia (BirdLife International 2017), which leads to its highly inter-annually fluctuating numbers in this region.

In addition, the Mongolian Gull that settled as a new breeder in studied marshlands was specific among the active defenders. In spite of its habitat preferences and colonial breeding similar to Black-headed Gull and Common Tern, it did not attract cryptic breeders, as did other active nest defenders. The reason lies probably in its size, associated with aggressiveness leading to increased risk of predation on nests or young among the nearest neighborhoods (Thomas 1972, Sládeček *et al.* 2014). Therefore, in such a poorer community with reduced protective umbrella, many cryptic breeders may feel more vulnerable and thus seek more intensely for the neighborhood of well-proven active defenders. We therefore

suggest that the spatial nest pattern of a bird community can change easily due to the natural dynamics of one or few fluctuating bird species acting as aggressive nest defenders, despite a relatively long-lasting stable habitat. The birds are probably largely versatile in respect of their nest placement, considering alternatives as habitat availability and potential neighbors.

Non-specified spatial effects in the models in both distinguished bird groups, active defenders and cryptic breeders, can have also other (mutually non-exclusive) explanations. First, individual variation in the propensity to aggregation and/or avoidance of neigborhood of nesting pairs might play a role; related birds may create many finer-scaled sub-aggregations across the area (Caro 2005), thus increasing the magnitude of spatial effects. Second, a certain inertia in choosing nest sites given the experience in previous nesting attempts (Doligez *et al.* 2002, Sebastián-González *et al.* 2010b) may influence decision making of individuals in the selection of nest locations. Third, we analysed the data on arbitrarily defined scale 100 × 100 m, but additional habitat factors could be revealed on finer or also coarser scales (Dray *et al.* 2012). Although the dbMEM method employed in our study comprises all spatial scales present in our data, the results are still affected by the 'grain size', i.e. the spatial resolution of analyzed data.

To conclude, besides the availability of specific habitats required by particular species to settle, the shared nesting was a general rule underlying the spatial arrangement of bird nests in large and pristine Siberian wetland. The spatial nest arrangement was driven by conspecific attraction among more abundant active nest defenders like gulls and terns, thus creating a protective nesting umbrella for many other cryptic breeders. The numbers instead of mere presence of active nest defenders contributed to spatial nest arrangement of cryptic breeders. The opportunity to juxtapose differently structured bird community in the same area in different years allowed us to show a stronger nest clumping in the year with impoverished community, probably resulting from increasing fear of predation risk. We suggest that significant decrease or disappearance of one or more abundant umbrella species may threaten the occurrence of accompanying cryptic breeders and reduce the overall bird diversity in the community. From the nature conservation standpoint it implies that support of abundant species with protective umbrella properties can be as important as the protection of their specific breeding habitat.

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Supporting Online Material

Supporting Information S1

Supporting Information S2

Supporting Information S3

Supporting Information S4

Supporting Information S5

Supporting Information S6

TABLES

Table 1. Partial RDA comparing the effects of habitat descriptors on nest abundance of active defenders in (A) 1993 and (B) 2013 using forward selection procedure with latitude used as a covariate.

(A) 1993

Predictor	Explains %	Contribution %	pseudo-F	P_{adj}
DivVeg	2.3	21.0	3.8	0.042
Moss	2.9	26.7	5.0	0.024
Deep	4.2	37.9	7.3	0.006
DistEdg			1.7	0.132
Wood			1.2	0.221
Wat			1.2	0.264

(B) 2013

Predictor	Explains %	Contribution %	pseudo-F	P_{adj}
Moss	5.1	44.7	8.6	0.005
DivVeg	4.3	38.2	7.7	0.008
Deep			1.2	0.275
Wat			0.9	0.302
Wood			0.9	0.276
DistEdg			0.7	0.493

Table 2. Variation partitioning results comparing adjusted variation in the community of active defenders explained by (a) habitats, (b) spatial predictors and (c) fraction shared by habitats and spatial predictors according to scheme in Supporting Information S3. Note that the Mean Square statistic uses the non-adjusted explained variation, divided by corresponding degrees of freedom (*DF*).

(A) 1993

Fraction	Variation	% Explained	% All	DF	Mean Square
a – Habitat effects	< 0.001	< 0.1	< 0.1	3	0.0024
b – Spatial effects	0.479	87.0	51.6	28	0.0191
c – Shared effects	0.071	13.0	7.7		
Total Explained	0.551	100	59.3	31	0.0201
All Variation	0.929		100	162	

Significance tests		
Tested Fraction	F	P
a+b+c	8.6	0.001
a+c	5.5	0.001
b+c	9.4	0.001

(B) 2013

Fraction	Variation	% Explained	% All	DF	Mean Square
a – Habitat effects	0.046	53.2	4.6	2	0.0283
b – Spatial effects	0.003	3.5	0.3	1	0.0086
c – Shared effects	0.037	43.4	3.7		
Total Explained	0.086	100	8.6	3	0.0342
All Variation	1.000		100	163	

Significance tests		
Tested Fraction	F	P
a+b+c	6.1	0.001
a+c	8.4	0.001
b+c	7.8	0.002

Table 3. RDA testing the effects of active defender descriptors on nest abundance of cryptic breeders using forward selection procedure.

(A) 1993

Predictor	Explains %	Contribution %	pseudo-F	P_{adj}
noAkt	3.1	90.8	5.1	0.017
presAkt			0.5	0.828

(B) 2013

Predictor	Explains %	Contribution %	pseudo-F	P_{adj}
AktNo	33.1	83.8	80.2	0.0002
Akt01	3.8	9.6	9.7	0.0012
Mon01	2.6	6.6	6.9	0.0020

Table 4. Variation partitioning results comparing adjusted variation in the community of cryptic breeders explained by (a) habitats, (b) neighbourhood of active nest defenders, (c) spatial predictors and (d-g) shared variation by (a)-(c) according to scheme in Supporting Information S3. Note that the Mean Square statistic uses the non-adjusted explained variation, divided by corresponding degrees of freedom (*DF*).

(A) 1993

Fraction	Variation	% Explained	% All	DF	Mean Square
a – Habitat effects	0.004	3.4	0.4	1	0.0092
b - Active defenders	0.021	17.8	2.1	1	0.0258
c – Spatial effects	0.047	39.9	4.7	3	0.0209
d	-0.001	-0.6	-0.1		
e	-0.001	-0.9	-0.1		
f	0.042	35.7	4.2		
g	0.006	4.9	0.6		
Total Explained	0.118	100	11.8	5	0.0289
All Variation	1.000		100	163	

Significance tests		
Tested Fraction	F	P
a+b+c+d+e+f+g	5.3	0.0002
a+b+d+e+f+g	7.2	0.0002
a+c+d+e+f+g	5.4	0.0002
b+c+d+e+f+g	6.2	0.0002
a+d+f+g	9.7	0.0002
b+d+e+g	5.1	0.0210
c+e+f+g	6.6	0.0002

Table 4. – continues

(B) 2013

Fraction	Variation	% Explained	% All	DF	Mean Square
a – Habitat effects	0.013	3.2	1.3	2	0.0099
b - Active defenders	0.324	79.8	32.4	3	0.1098
c – Spatial effects	-0.001	-0.2	-0.1	1	0.0029
d	0.020	5.0	1.5		
e	0.002	0.6	2.0		
f	0.011	2.6	0.2		
g	0.037	9.0	3.7		
Total Explained	0.407	100	40.7	6	0.0714
All Variation	1.000		100	163	

Significance tests		
Tested Fraction	F	P
a+b+c+d+e+f+g	19.6	0.0002
a+b+d+e+f+g	23.4	0.0002
a+c+d+e+f+g	5.9	0.0004
b+c+d+e+f+g	27.5	0.0002
a+d+f+g	8.1	0.0004
b+d+e+g	34.8	0.0002
c+e+f+g	9.4	0.0006

FIGURES

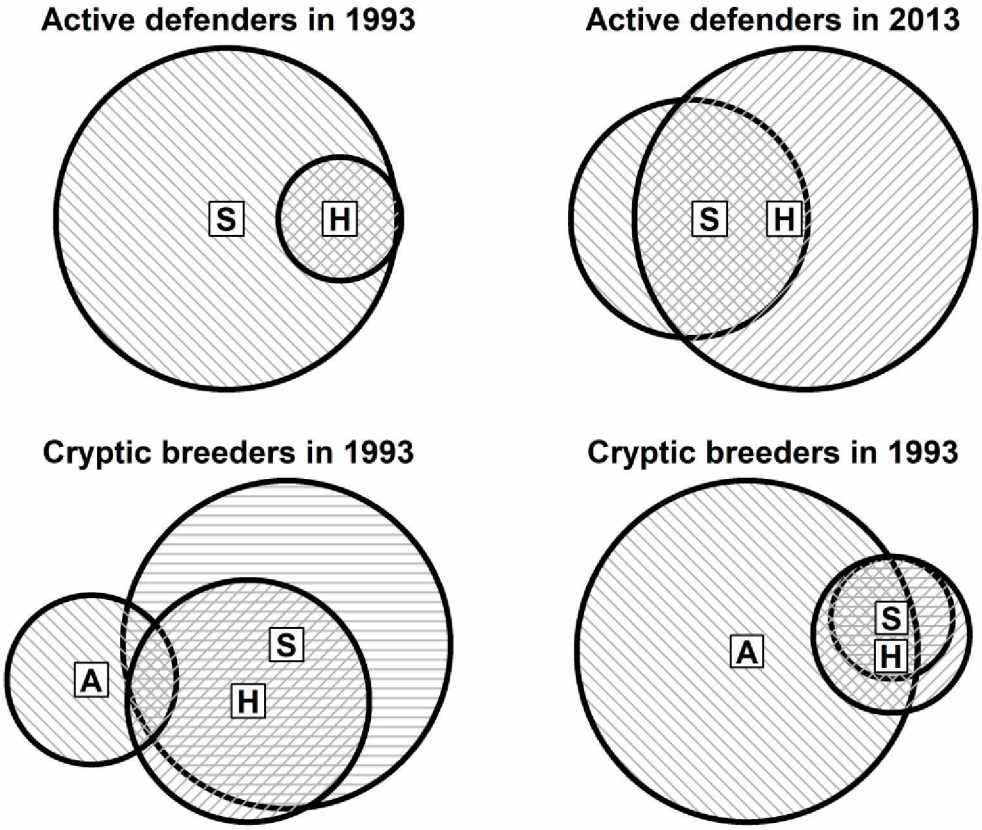


Figure 1. Graphical summarizing of unique (exclusive) and shared partial effects in variation partitioning for the effects on nest pattern using Venn diagrams. Habitat (H) and space (S) are included as predictors in active nest defenders, while habitat (H), space (S) and active defenders (A) are used as predictors in cryptic breeders.

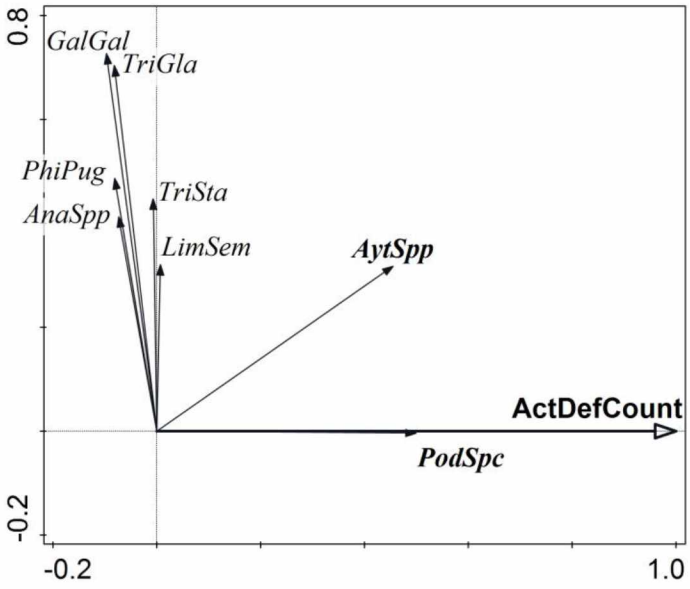


Figure 2. Responses of cryptic breeders to abundance of active nest defenders in 1993. Ordination diagram shows the first two axes of partial RDA, where the first (horizontal) axis is constrained by *ActDefCount* variable and explains 2.5% ($R^2_{adjusted}$) of the total variation. The second unconstrained axis explains 30.1% of the total variation. Two bird taxa responding to *ActDefCount* variable are shown in bold.

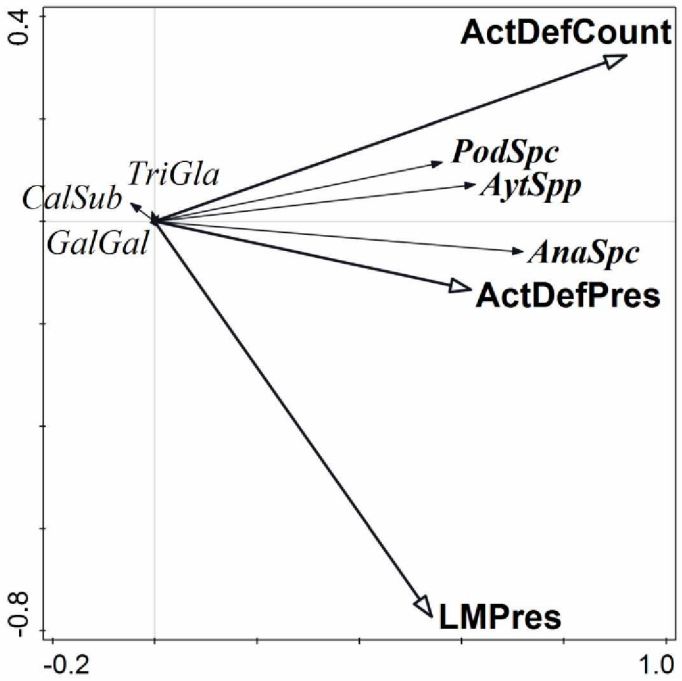
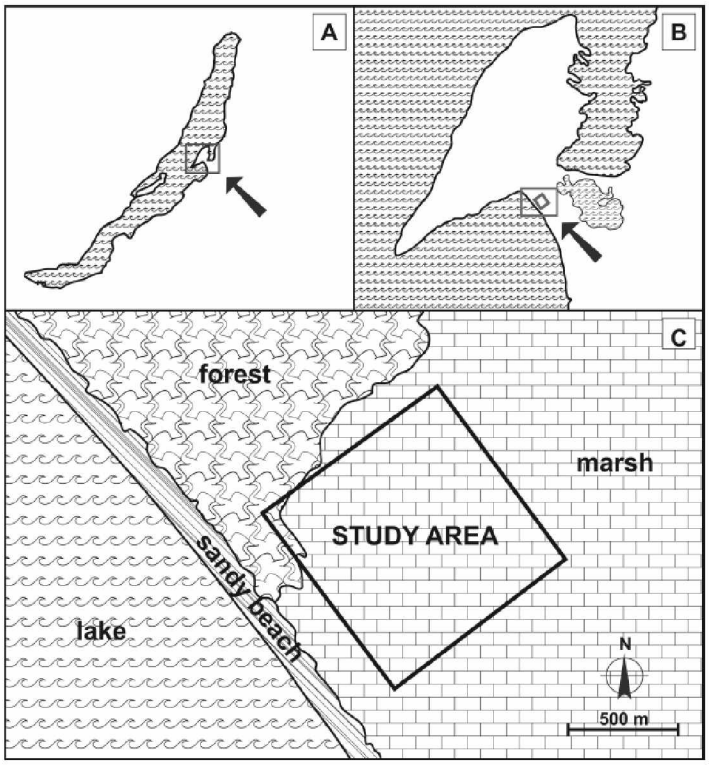


Figure 3. Responses of cryptic breeders to presence and coloniality of active nest defenders in 2013 indicating different trends of behaviour in greebes and ducks (positive response) versus waders (no response). The diagram shows the first two axes of partial RDA, explaining together 38.2% ($R^2_{adjusted}$) of the total variation. Three bird taxa responding to selected descriptors of active defenders are shown in bold.

Supporting Information S1

A | Location of the study area on the isthmus of the Svjatoj Nos Peninsula, Lake Bajkal, Russia. A) Lake Bajkal, B) Isthmus of the Svjatoj Nos Peninsula, C) Position towards the lake coast and forest (Sládeček *et al*. 2014).



B| Situation photo of the study area (yellow) from the northwest direction in June 1993.

Supporting Information S2

A| Four main habitats distinguished in the study area

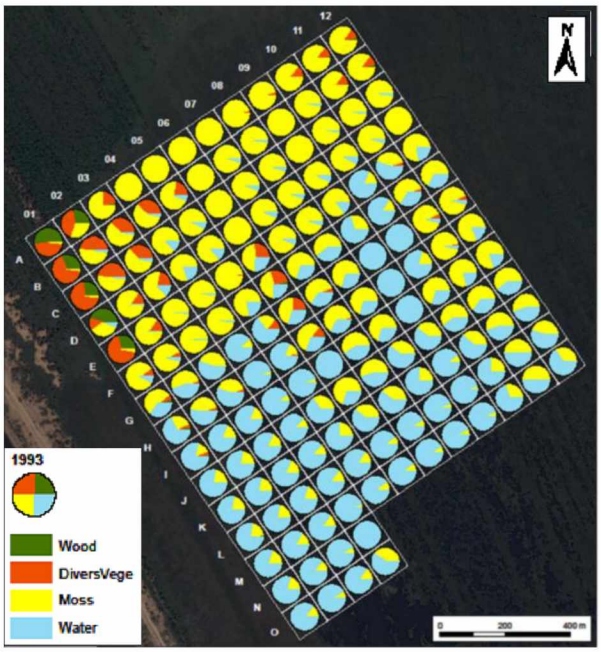
Type	Description	Plant dominants	Cover (%)		
			Plants	Moss	OldGrass
Wood	Groups of trees with > 2 m of height on transition between taiga and swamps	*Betula pendula*, *Pinus sylvestris*, *Empetrum nigrum*, *Vaccinium* spp., *Chamaedaphne calyculata*, *Salix* spp.	70-100	10-50	10-50
DiversVeget	Sedges or bush-grass tufts with height 50-90 cm, relatively dry, passable wet surface, somewhere with dwarf willows (*Salix myrtilloides*)	*Comarum palustre*, *Salix myrtilloides*, *Calamagrostis purpurea*, *Carex chordorrhiza*, *Lysimachia thyrsiflora*	40-80	50-90	20-70
Moss	Moss dominated and 10-20 cm tall sparse uniform cover or with *Sparganium natans* and *Calla palustris* on highly wet sites lacking open water	*Sparganium natans*, *Calla palustris*, *Menyanthes trifoliata*, *Carex limosa*, *C. lasiocarpa*, *C. diandra*, *Eriophorum gracile*	30-80	80-90	0-10
Water	Continuous open water without or with submerged moss, somewhere with emergent plant cover; interspersed with floating islands with aquatic vegetation	*Sparganium natans*, *Potamogeton gramineus*, *P. compressus* (submergent), *Nymphaea tetragona*, *Utricularia vulgaris*, *Menyanthes trifoliata* (emergent)	0-50	0-20	0-10

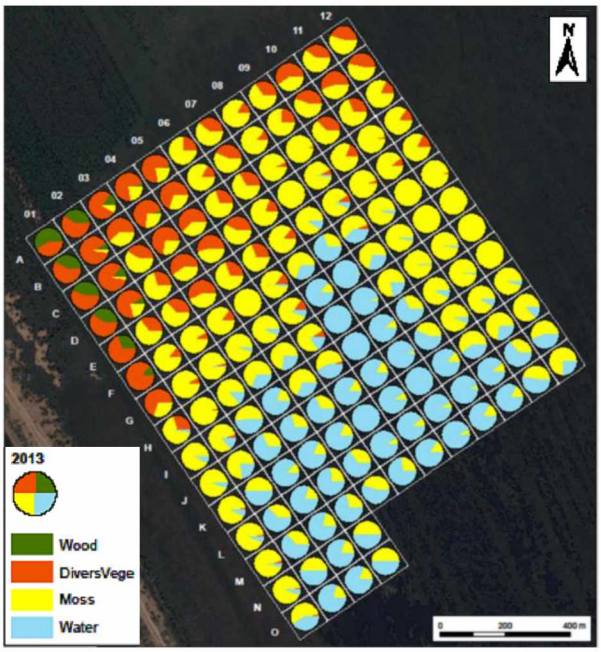
B| Four main habitats distinguished in the study area (photo by Vojtěch Kubelka)

Wood (above) Moss (below)

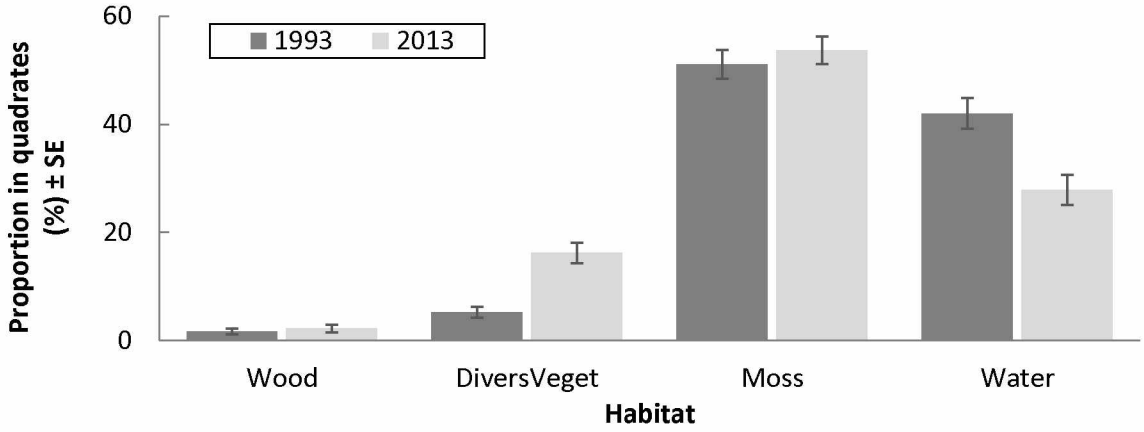
DiversVeget (above) Water (below)

C| Proportion of four main habitats in the squares under study within a real terrain map projection

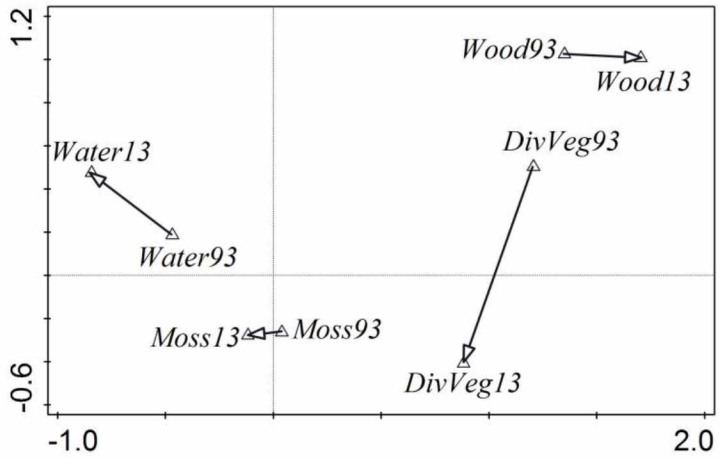




D| Proportion of four main habitats in the squares under study

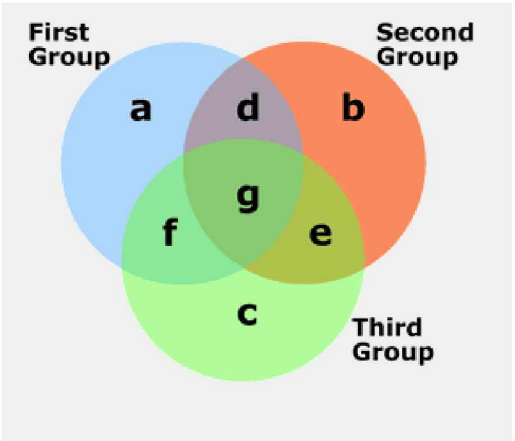


E| First two axes of correspondence analysis (CA) comparing the change in the proportions of habitat categories within quadrats between 1993 and 2013. The percentage cover of each habitat type estimated separately in each year was used as response variables (2 × 4 habitat types). Whereas proportion of moss remained relatively stable, diversified vegetation dominated with Carex (DiverVeget) changed more strongly. Changes in Water and Wood were of intermediate extent. Displayed axes explain together 80.4% of the total variation in habitat proportions.



Supporting Information S3

Graphical symbolizing of unique (exclusive) and shared partial effects in variation partitioning for the effects on nest pattern in cryptic breeders using Venn diagrams. Only the First Group (Habitat) and Third Group (Space) of predictors are included in active nest defenders.



First Group - Habitat

a - unique effect, *a+d+f+g* – total/shared effect

Second Group - Active nest defenders

b - unique effect, *b+d+g+e* – total/shared effect

Third Group – Space

c - unique effect, *c+f+g+e* – total/shared effect

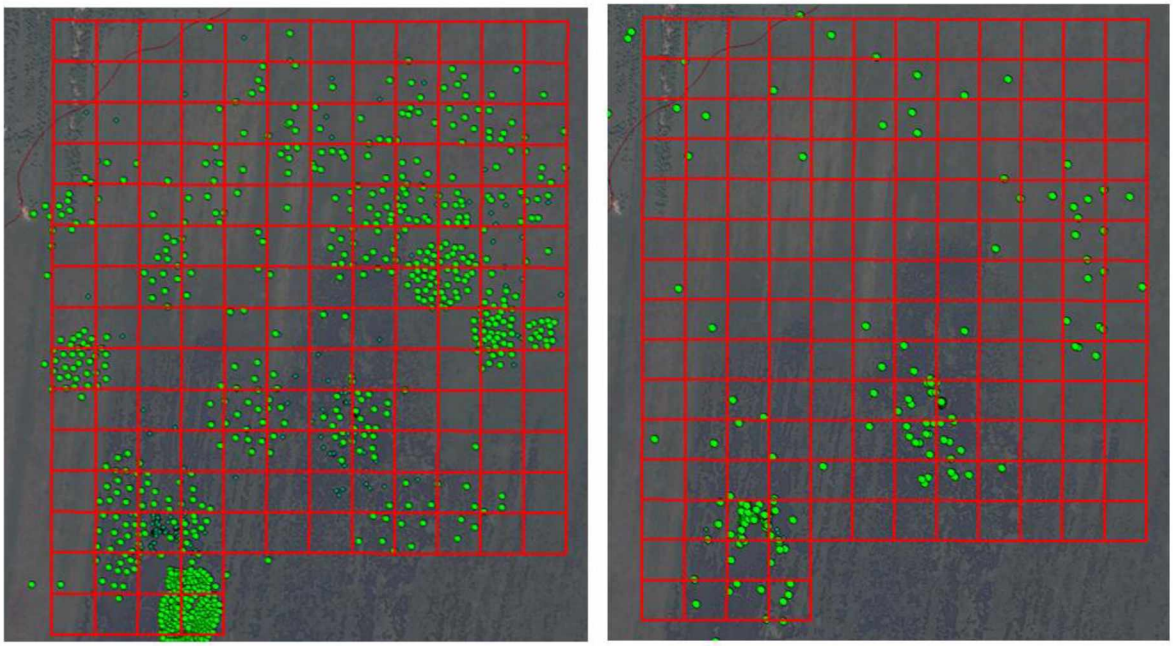
Supporting Information S4

A | List of species with numbers of confirmed or probable nests included in analysis. A = active nest defenders, AP = active defender and potential nest predator Mongolian Gull *Larus mongolicus*, C = cryptic breeders. Grey font indicates namely identified species but included in analysis only as a part of summarized '***Spc' group. Indicated abbreviations are used in ordination diagrams.

Species	Abbreviation	role	1993	2013
Chlidonias leucopterus	ChlLeu	A	297	0
Chroicocephalus ridibundus	LarRid	A	165	68
Hydrocoleus minutus	LarMin	A	28	0
Larus canus	LarCan	A	27	0
Sterna hirundo	SteHir	A	14	11
Vanellus vanellus	VanVan	A	11	8
Numenius arquata	NumArq	A	4	6
Chlidonias hybrida	ChlHyb	A	1	0
Larus mongolicus	LarMon	AP	0	10
Anas platyrhynchos		C	6	5
Anas acuta		C	3	2
Anas clypeata		C	0	1
Anas sp.		C	2	32
Anas sp.	AnaSpc	C	11	40
Anas crecca	AnaCre	C	1	0
Aythya fuligula		C	1	17
Aythya ferina		C	6	1
Aythya sp.		C	1	2
Aythya sp.	AytSpc	C	8	19
Tringa glareola	TriGla	C	25	4
Gallinago gallinago	GalGal	C	20	3
Tringa stagnatilis	TriSta	C	18	2
Philomachus pugnax	PhiPug	C	12	2
Limnodromus semipalmatus	LimSem	C	11	0
Calidris subminuta	CalSub	C	2	4
Podiceps auritus		C	3	3
Podiceps grisegena		C	2	4
Podiceps sp.		C	0	1
Podiceps sp.	PodSpc	C	5	8
Porzana pusilla	PorPus	C	2	1
Gavia arctica	GavArc	C	1	1
Gavia stellata	GavSte	C	1	0
Rallus aquaticus	RalAqu	C	1	0

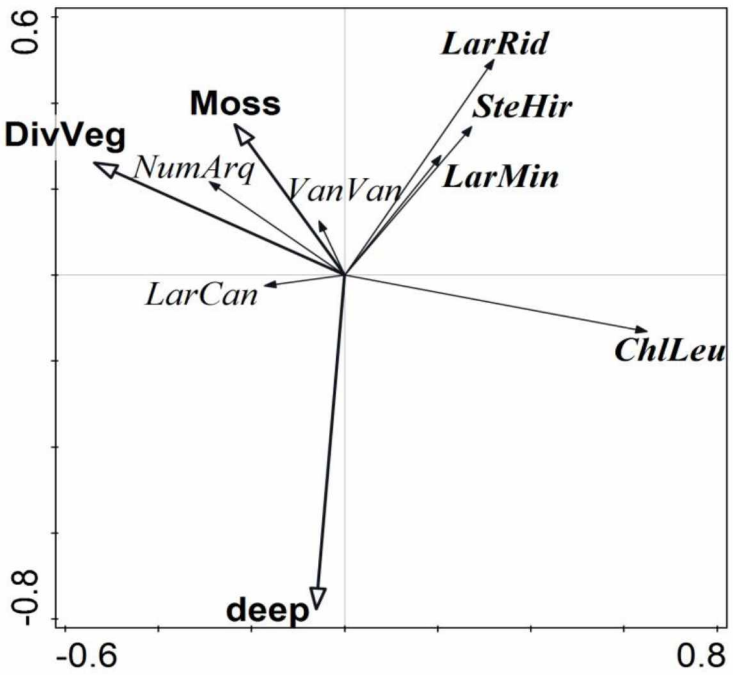
B | Nest spatial patterns (all species) across the study area. High aggregation is evident in both years.

1993 2013

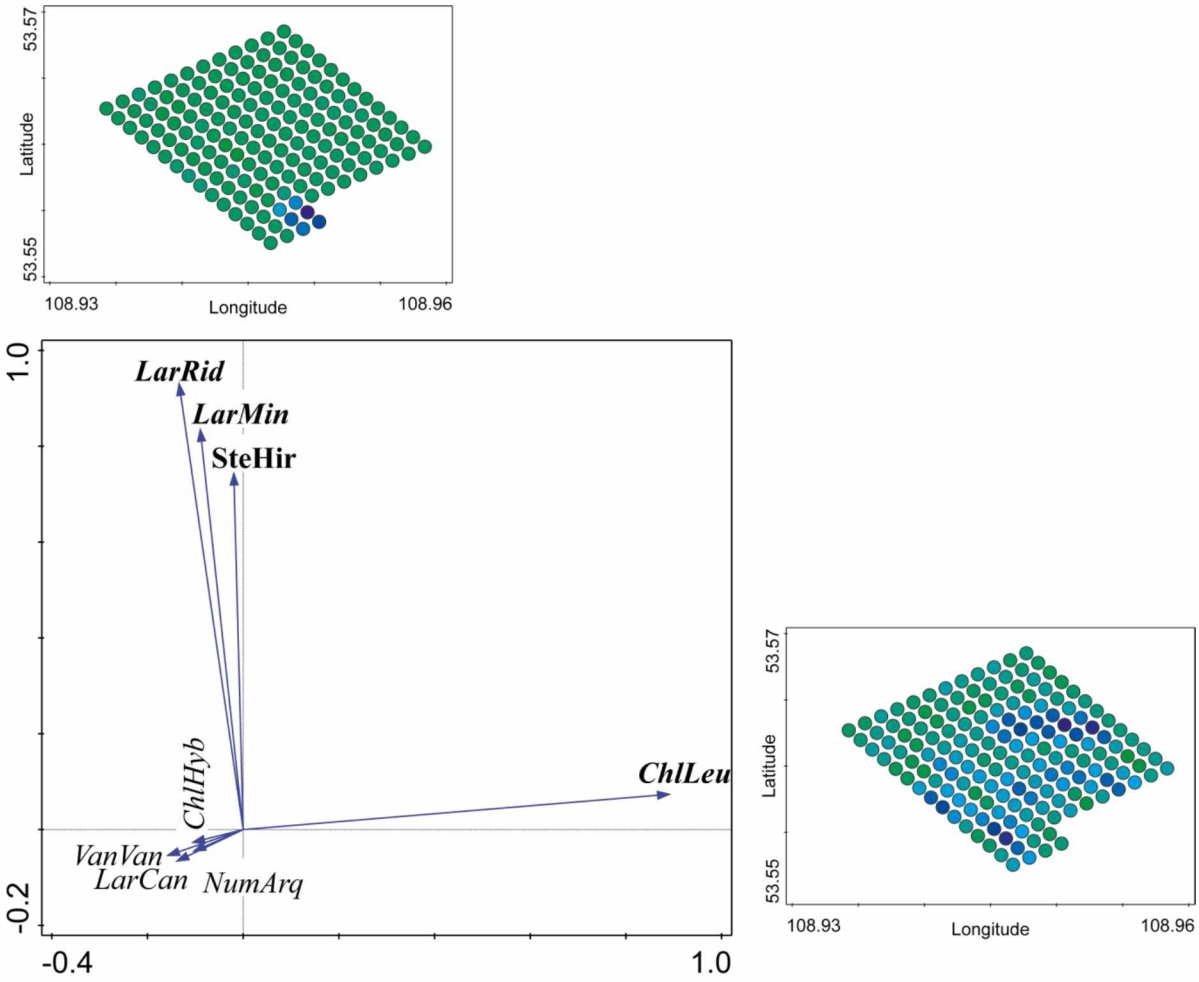


Supporting Information S5

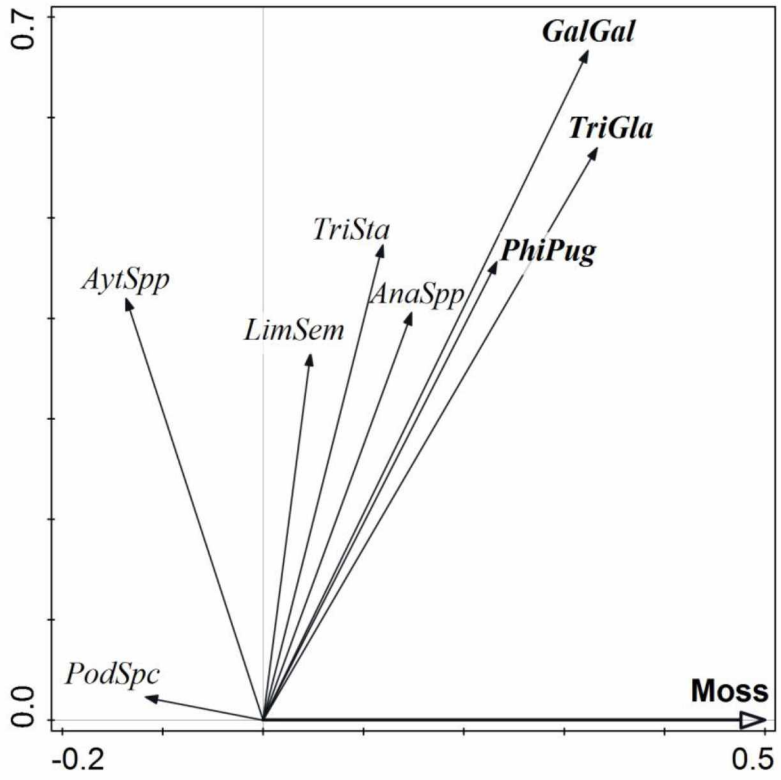
A | Habitat association of active nest defenders in 1993 indicating a general avoidance of areas with deep water and trend in waders to inhabit diverse vegetation and moss habitats unlike larids. Ordination diagram shows the first two axes of partial RDA, explaining 7.7% ($R^2_{adjusted}$) of the total variation. Four bird species responding to at least one of the three chosen habitat descriptors are shown in bold, only *Chlidonias leucopterus* responds to all three predictors.



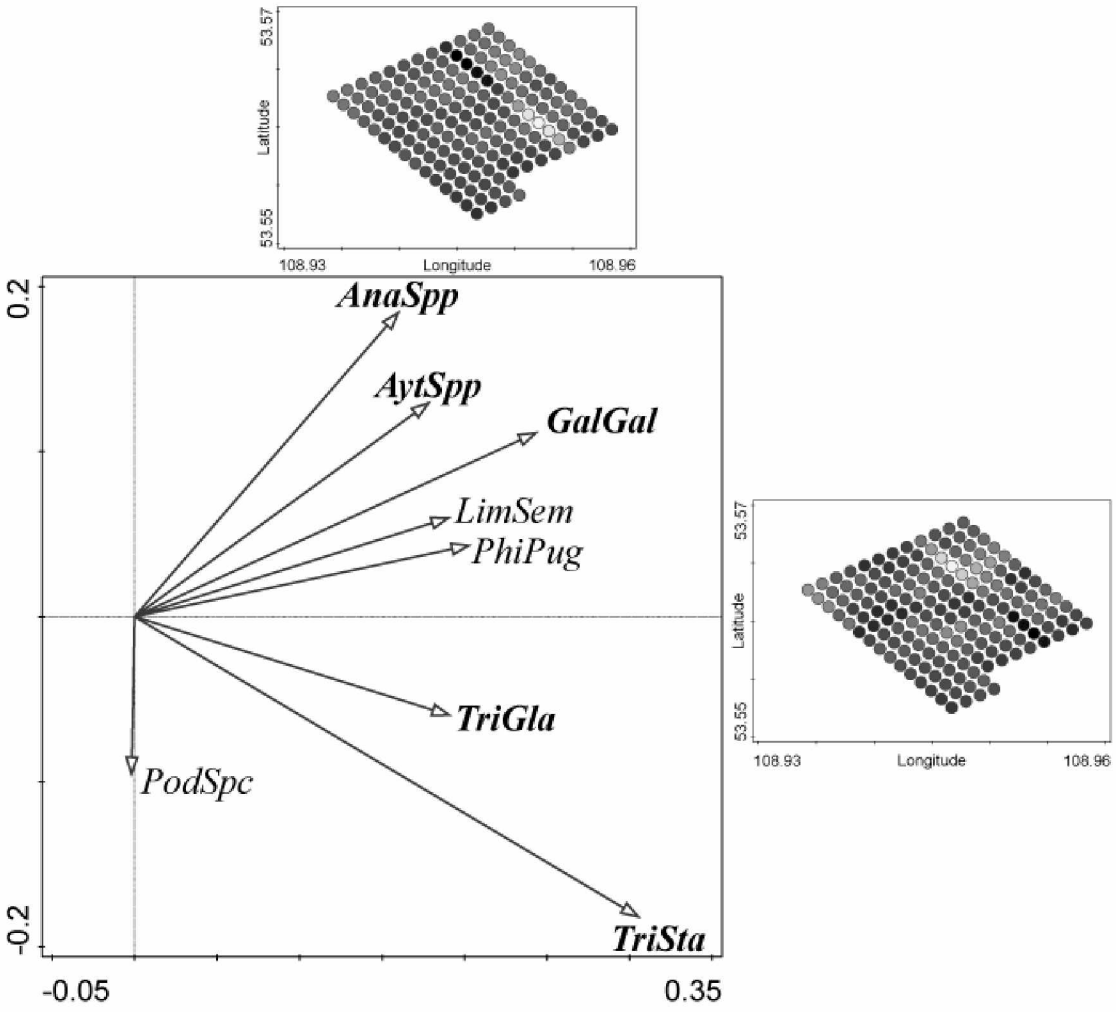
B | Association of active nest defenders with spatial predictors in 1993 indicating similar spacing of three larids creating shared colonies and *Chlidonias leucopterus* with different spatial behaviour. The meaning of the first two ordination axes (explaining, respectively, 35.2% and 26.8% of the total community variation, for horizontal and vertical axis) is illustrated by the two inset XY diagrams. They show the positions of grid squares (located in the graph according to their geographical position) on the respective constrained axis with the circle shade level: white corresponds to largest positive position, while black represents the most negative position. This suggests the location of larid nests in the southermost corner of the research area, while the nests of *Chlidonias leucopterus* are spread across the south-west half of the study area. Three species with short arrows pointing to lower left corner have very small amount of their variation explained by spatial predictors (<3%).



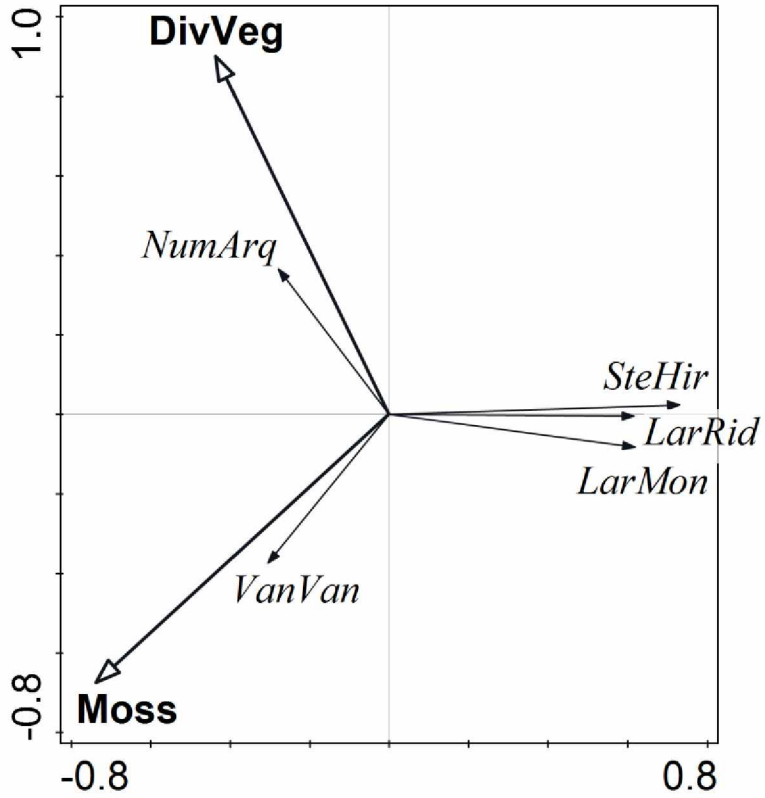
C | Response of cryptic breeders community to variation in *Moss* habitat proportion in 1993. Ordination diagram shows the first two axes of partial RDA, where the first (horizontal) axis is constrained by *Moss* and explains 5.1% ($R^2_{adjusted}$) of the total variation. The second unconstrained axis explains 25.6% of the total variation. Three bird species responding to *Moss* variable are shown in bold.



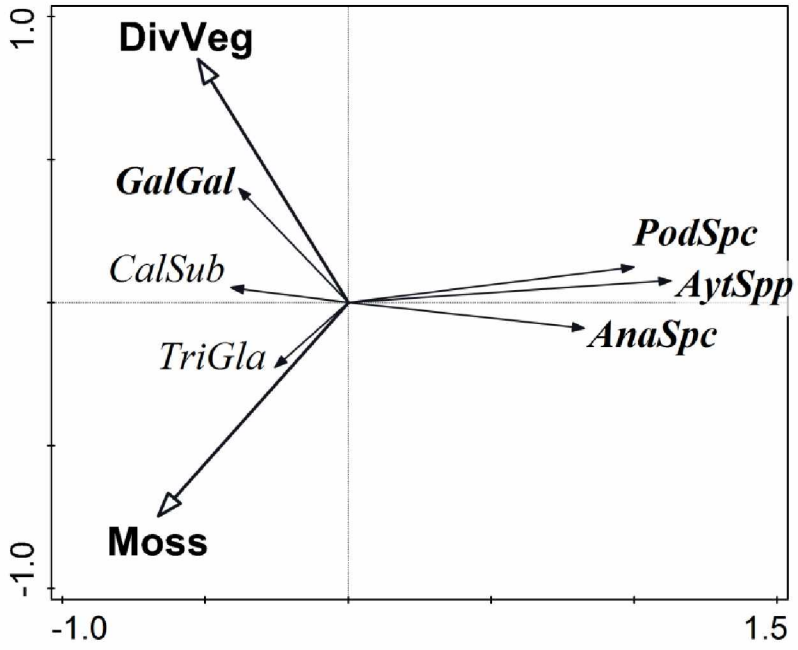
D | Association of cryptic breeders with spatial predictors in 1993 indicating their tendency to join/separate occurrences regardless of habitat. The meaning of the first two ordination axes (explaining, respectively, 3.8% and 1.1% of the total community variation, for horizontal and vertical axis) is illustrated by the two inset XY diagrams. They show the positions of grid squares (located in the graph according to their geographical position) on the respective constrained axis with the circle shade level: white corresponds to largest positive position, while black represents the most negative position. Bird taxa responding to at least one of the three selected spatial predictors (latitude and two spatial eigenvectors) are shown in bold. The spatial response of *Tringa glareola* and *Tringa stagnatilis* was different from the other three responsive taxa.



E | Habitat preferences of active nest defenders in 2013. Ordination diagram shows the first two axes of partial RDA, explaining 8.3% ($R^2_{adjusted}$) of the total variation. Curlew is positively related to *DivVeg* habitat cover, lapwing to *Moss* habitat cover, while the larids tend to avoid both habitat types.



F | Habitat association of cryptic breeders in 2013 indicating diferent trends in ducks and greebes vs. waders. Ordination diagram shows the first two axes of partial RDA, explaining together 8.1% ($R^2_{adjusted}$) of the total variation. Four bird taxa responding to one or both selected habitat descriptors are shown in bold, with the three arrows pointing to right representing taxa partly avoiding both selected habitat types.



Supporting Information S6

A | Partial RDA comparing the effects of individual spatial predictors on nest abundance of active defenders in (a) 1993 and (b) 2013 using forward selection procedure. Note that latitude was used as a covariate in 1993, but it is (as the only significant spatial predictor) explicitly included in overview for 2013. Only the selected spatial predictors (with significant conditional effects) are shown in the table.

(a) 1993

Predictor	% Explained	% Contrib.	F	P_{adj}
PCO.39	4.6	5.5	7.8	0.025
PCO.24	4.7	5.6	8.3	0.025
PCO.26	4.0	4.7	7.3	0.019
PCO.62	3.8	4.5	7.3	0.038
PCO.58	3.7	4.4	7.3	0.030
PCO.13	3.2	3.8	6.6	0.038
PCO.28	3.1	3.7	6.5	0.030
PCO.14	3.1	3.6	6.7	0.025
PCO.25	2.9	3.5	6.6	0.028
PCO.38	2.7	3.2	6.4	0.022
PCO.48	2.5	2.9	6.0	0.017
PCO.49	2.4	2.8	6.0	0.030
PCO.5	2.3	2.7	6.0	0.043
PCO.69	2.1	2.6	5.8	0.025
PCO.61	2.1	2.5	5.8	0.025
PCO.42	2.1	2.4	5.9	0.027
PCO.68	1.9	2.3	5.7	0.017
PCO.53	1.9	2.2	5.7	0.027
PCO.40	1.5	1.8	4.9	0.034
PCO.43	1.5	1.8	4.9	0.031
PCO.72	1.5	1.7	4.9	0.025
PCO.22	1.4	1.6	4.7	0.024
PCO.34	1.3	1.6	4.6	0.030
PCO.10	1.2	1.5	4.4	0.022
PCO.9	1.2	1.5	4.6	0.022
PCO.4	1.4	1.7	5.3	0.020
PCO.51	1.2	1.4	4.6	0.028
PCO.15	1.1	1.3	4.4	0.031

(b) 2013

Predictor	% Explained	% Contrib.	F	P_{adj}
lat-C	5.5	8.7	9.4	0.0416

B | RDA comparing the effects of habitat descriptors on nest abundance of cryptic breeders in (a) 1993 and (b) 2013 using forward selection procedure.

(a) 1993

Predictor	Explains %	Contribution %	pseudo-F	P_{adj}
Moss	5.7	66.0	9.7	< 0.001
Deep			1.6	0.150
DistEdg			0.9	0.470
Water			0.8	0.530
Wood			0.7	0.469
DivVeg			0.6	0.638

(b) 2013

Predictor	Explains %	Contribution %	pseudo-F	P_{adj}
Moss	4.1	39.4	6.9	0.003
DivVeg	5.1	49.2	9.0	0.002
Wood			1.0	0.334
Water			1.0	0.301
Deep			0.8	0.474
DistEdg			0.5	0.685

C | RDA comparing the effects of individual spatial predictors on nest abundance of cryptic breeders in 1993 using variation forward selection procedure. Except latitude (F = 7.8, P = 0.001), no further predictor was significant in 2013. Only the selected spatial predictors (with significant conditional effects) are shown in the table.

Predictor	% Explained	% Contrib.	F	P_{adj}
lat-C	5.7	9.7	9.7	0.0156
PCO.18	3.2	5.4	5.6	0.0364
PCO.52	2.2	3.8	3.9	0.0312

Black-winged Pratincole (*Glareola nordmanni*) at a saline lake in Astrakhan, Russia 2017

Chapter 9

Alarmingly high nest predation in shorebirds associations at Caspian steppe lakes

Vojtěch Kubelka, Jiří Mlíkovský, Veronika Zavadilová, Milan Frencl, Kirill Litvinov & Miroslav Šálek

(under the review)

Alarmingly high nest predation in shorebirds associations at Caspian steppe lakes

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Nest predation is the most important cause of breeding failure to which shorebirds have invented many anti-predatory strategies. Among them breeding in dense colonies with active defence and use of "protective umbrella" from breeding species actively repelling predators are perceived as successful tactics. However, there are potential drawbacks if predators are efficient and focused on breeding colonies. To extend our knowledge on breeding productivity in inter-specific associations, we investigated shorebirds colonies at steppe lakes near Astrakhan in Russia during May 2017 and we report exceptionally high daily nest predation (0.106) in 59 nests of seven shorebirds species at five localities. In three most abundant species, 96% of nests were predated in Black-winged Pratincole *Glareola nordmanni*, 92% in Black-winged Stilt *Himantopus himantopus* and 98% in Pied Avocet *Recurvirostra avosetta*. Terns in the same colonies initiated their incubation earlier than shorebirds, suggesting that shorebirds were generally attracted into heterospecific colonies during incubation of terns to benefit from the "protective umbrella" against predators. However, total nest predation in Common Tern *Sterna hirundo* was also high (91%) and therefore questioning anti-predatory benefits of such breeding associations. Our results illustrate that even dense breeding colonies of shorebirds breeding in natural steppe lakes together with terns can experience an exceptionally high nest predation. Further studies from this region are needed to find out whether high nest predation was a seasonal anomaly or whether it represents a widespread phenomenon with possible detrimental consequences for shorebirds' population dynamics.

Keywords: anti-predator behaviour, Charadrii, colonial breeding, *Glareola nordmanni*, *Himantopus himantopus*, nest predation, nest scrape reuse, "protective umbrella" hypothesis, *Recurvirostra avosetta*, Russia, waders

INTRODUCTION

Anti-predatory breeding associations among shorebirds or between shorebirds and terns or gulls represent an obvious and interesting phenomenon (Gochfeld 1984, Quinn & Ueta 2008, Colwell 2010). This behaviour consists of i) seeking for the presence of other conspecific, often active defenders, in the breeding colony (Hegyi & Sasvári 1997, Šálek & Šmilauer 2002, del Hoyo *et al.* 2017) or ii) seeking for "protective umbrella" from active nest defender for less aggressive species (e.g. Bub 1957, Nankinov 1978, Dyrcz *et al.* 1981, Larsen & Moldsvor 1992, Powell 2001, Nguyen *et al.* 2006, Kubelka *et al.* 2014, Sládeček *et al.* 2014).

Both tactics are generally appreciated as successful anti-predatory strategies reducing nest or offspring predation rates (Haemig 2001, Quinn & Ueta 2008, Sládeček *et al.* 2014). On the other hand, conspicuous breeding associations can be targeted by effective predators rendering similar associations no longer beneficial from nest predation perspective (Caro 2005, McKinnon *et al.* 2013, Giroux *et al.* 2016). Despite many studies, costs and benefits of breeding associations for protective and protected species are still not fully understood (Quinn & Ueta 2008), provoking further research in different habitats and geographic locations.

So far, closer investigation of inter-specific breeding associations in steppe habitat with consequences for reproductive output has been missing. To address this knowledge gap, here we describe species composition, incubation start timing and nest predation patterns in breeding associations of shorebirds and terns at steppe lakes in Astrakhan region.

METHODS

Study area and data collection

We collected all data presented here during 15–24 May 2017 at five localities in Astrakhan steppe region in Russia (Fig. 1, Table 1). We searched for the breeding associations of shorebirds and terns in steppe landscape. Apart from the first locality, a bottom of an empty dam with fresh water pools and sparse reeds, all localities were natural lakes in open steppe with different salinity and corresponding vegetation being sparser and shorter near salt lakes. Surrounding countryside was open steppe, often dominated by different plant species, regularly used for extensive grazing and locally interrupted with villages, farms and irrigated fields. We found no marks of direct human persecution of breeding birds at any locality. Birds were breeding on the banks around lakes up to 30 m from the lake, only Promyslovka East consisted of island breeding colony of shorebirds and terns. In Promyslovka South, there were two breeding colonies of shorebirds and terns, the first located on the lake bank and the second on the island 200 m apart from the first colony. The distance between neighbouring nests of shorebirds or terns was normally 2–10 m, rarely 10–50 m. The distance among five localities was 9–125 km.

We located nests in the colonies by the scope or binoculars from distance. Then we found nests by the closer investigation of the breeding ground in the team of 2–4 people. We took GPS coordinates of every nest and placed a small wooden popsicle 1.5 m from each nest for

easier nest relocation. We took eggs measurement (length, width) to the nearest 0.05 mm using a vernier calliper and we estimated the day of incubation start for each nest with known sequence of egg-laying or with use of flotation method (van Paassen *et al.* 1984) adjusted to the species-specific incubation periods (Myhrvold *et al.* 2015). We visited a majority of the nests repeatedly and determined the fate of each nest. We recorded three possible outcomes, nest 1) survived the observation period; 2) was depredated (missing eggs prior expected hatching or present remnants of predated eggs); 3) was abandoned. We did not detect any other nest failure (e.g. flooding, trampling or agriculture machinery). Several nests found during the last visit of three localities were not included in the nest predation analysis.

Data processing

We used two measures of nest predation in the study. First, daily nest predation rate of nests according to Mayfield defined as the number of predated nests divided by the exposure of all nests in days (Mayfield 1961, 1975) providing values standardized among species and locations (Ricklefs 1969). We calculated the standard error for each species following Johnson (1979). Second, we computed total nest predation rate of the nests as 1-((1-daily nest predation rate)$^{\text{incubation period}}$), where incubation period means the total length of egg-laying and incubation period in days for particular species (Mayfield 1961, 1975). Since egg-laying and incubation period represent the interval for which the successful nest with eggs is exposed to potential predators, the total nest predation rate gives species-specific nest predation rate (mean percentage of nests being depredated in particular population) from life history perspective (Kulesza 1990, Stutchbury & Morton 2001). We extracted egg-laying and incubation periods from Myhrvold *et al.* (2015). We refer to these variables through the article as daily nest predation and total nest predation, the later expressed between 0% and 100%.

The procedure of computing the exposure for daily nest predation is defined as follows. The exposure for survived nests is from a day of finding until the last visit (e.g. 16 May and 24 May means 24-16 = eight days of exposure). The exposure for depredated nests is from the day of finding until midpoint assumption between last positive and first negative visits of the particular nest. Only complete nest depredations were included in the predated nests category (partial egg loss were omitted). All four abandoned nests, the most probably as a result of partial egg-predation, were omitted from further nest predation analyses.

For testing incubation start date differences between shorebirds and terns (Fig. 2), we used linear mixed-effect model (Crawley 2013) with a random effect of the breeding colony. The linear mixed-effect model was fitted with the 'lme4' package (Bates & Maechler 2012) and the test was two-tailed.

RESULTS

We found 78 nests of seven shorebird species in six dense breeding colonies at five localities (Table 1, Table 2). The mean incubation start date for shorebirds varied between 6 and 24 May (Table 2) and in comparison with terns was on average by 1.5 days later (Fig. 2), the

difference was marginally non-significant (LME; $\chi^2 = 2.88$; df = 1; P = 0.09). Nest predation rates were consistently high for all species of shorebirds apart from Common Redshank (*Tringa totanus*) with only one nest found (Table 3). Daily nest predation was also high for all localities with an exception of Promyslovka east where only three nests of Pied Avocet (*Recurvirostra avosetta*) were shortly monitored. Daily nest predation was high for both nest locations: mainland vs. island (Table 4). For Common Tern *Sterna hirundo*, daily nest predation was 0.091 ± 0.043 (SE), total nest predation was 91% (exposure = 44 days, four nests from 11 were depredated). As potential nest predators we recorded once Red Fox *Vulpes vulpes* directly searching in the breeding colony, we observed several times Western Marsh Harriers *Circus aeruginosus* and Hooded Crows *Corvus cornix* in the close vicinity of breeding grounds of shorebirds. Furthermore, we saw Eurasian Magpies *Pica pica*, Rooks *Corvus frugilegos* and Western Jackdaws *Corvus monedula* and Montagu's Harrier *Circus pygargus* in the surrounding landscape. We recorded an interspecific nest scrape reuse in shorebirds once, when in the nest of Black-winged Stilt *Himantopus himantopus* with three eggs in Liman locality we found two fresh eggs of Black-winged Pratincole *Glareola nordmanni* on the subsequent visit five days later.

DISCUSSION

We report unusually high nest predation rates for shorebirds breeding at steppe lakes in Astrakhan region. The total nest predation of 92–98% for three the most abundant shorebirds species means that very low numbers of chicks in Black-winged Pratincole, Black-winged Stilt and Pied Avocet could be hatched. Even with improbable 100% chick survival, the overall breeding productivity would be low. Such unfavourable conditions over several seasons could have a detrimental effect on species population dynamics (Evans & Pienkowski 1984, Colwell 2010). Currently, Black-winged Pratincole population is described as a slightly decreasing (BirdLife International 2015) or stable (Mishchenko 2017) species in European Russia. Black-winged Stilt is slightly increasing (BirdLife International 2015, Mishchenko 2017), and Pied Avocet is a species with stable or fluctuating populations (BirdLife International 2015, Mishchenko 2017).

Similarly high nest predation rates (0.085–0.201 in terms of daily nest predation and 92.3–99.7% for total nest predation) have been recorded only ten times out of 237 investigated shorebirds populations through the world (Kubelka *et al.*, unpubl. data). Historically, such high nest predation rates were recorded for Wilson's Phalarope *Steganopus tricolor* in North Dakota (Kagarise 1979), for Common Ringed Plover *Charadrius hiaticula* in the United Kingdom (Pienkowski 1984) and for Whimbrel *Numenius phaeopus* in Norway (Larsen & Moldsvor 1992). Recently, five Arctic species, Pacific Golden Plover *Pluvialis fulva*, Pectoral Sandpiper *Calidris melanotos*, Sharp-tailed Sandpiper *Calidris acuminata*, Little Stint *Calidris minuta* and Ruff *Calidris pugnax* are experiencing such high nest predation rates at Taimyr peninsula in Russia (Soloviev *et al.* 2010, Arctic Shorebird Demographics Network 2016, M. Soloviev in litt. 2016) as well as Eurasian Oystercatchers *Haematopus ostralegus* in Sweden (Ottvall 2005) and Black-tailed Godwits *Limosa limosa* breeding at Lake Baikal in Russia (Groen *et al.* 2006).

The recorded high nest predation rates for Black-winged Pratincole, Black-winged Stilt and Pied Avocet in Astrakhan region correspond with recently reported high nest predation rates of these species in other parts of Russia. Despite a general lack of nest predation data from the Caspian lake region, comparison can be made with Sociable Lapwing *Vanellus gregarius* breeding in steppe near Korgalzhyn and Pavlodar in Northeast Kazakhstan, experiencing also quite high total nest predation, 51% and 71% respectively (Watson *et al.* 2006, Sheldon *et al.* 2013, P. Donald, R. Sheldon in litt. 2016). On the other hand, only 43% of nest were depredated in Eurasian Oystercatchers breeding at Black Sea coast in Ukraine (Rudenko 1998). From numbers of fledged juveniles, it can be assumed that nest predation had to be much lower in Northeast Kazakhstan in 2006 and 2007 (Kamp *et al.* 2009) than in Astrakhan region in 2017.

Without knowing the temporal variation of nest predation rates and predator abundances over longer period in Astrakhan region, we can only assume possible factors generating such high nest predation in this case study. During our fieldwork, we encountered signs of nest predation by mammals as well as by birds according to Green *et al.* (1987) suggesting combine effect of more predator species. We often found these signs on the first visit of the breeding ground indicating that intense nest predation had been already happening prior our visit, therefore we suggest that our short presence in the colonies should not meaningfully affect nest predation rates.

The high nest predation in Astrakhan region could be linked to a rise of predator densities, similarly to Western Europe (MacDonald & Bolton 2008, Roodbergen *et al.* 2012). Indeed, there was recorded 9% increase in estimated Red Fox abundances over two years: 12,500 ex. in 2008, 12,700 ex. in 2009 and 13,600 ex. in 2010 for whole Astrakhan region (Zvolinskiy *et al.* 2016). However, authors mentioned a strong decline of foxes after the year 2010 for unknown reason (Zvolinskiy *et al.* 2016) and we do not know numbers of foxes for 2016–2017. Other two mammalian predators, Wolf (*Canis lupus*) and Golden Jackal (*Canis aureus*) should be increasing in numbers in Astrakhan region (Zvolinskiy *et al.* 2016). Also, Belik & Lebedeva (2004) reported increased predation pressure, namely from corvids in the Species Action Plan for Black-winged Pratincole. Further, Kamp *et al.* (2009) were suggesting foxes and hedgehogs as important nest predators of this species. Kamp *et al.* (2009) were also discussing increased nest predation by small carnivores in the year with a low abundance of voles. A tight connection between voles abundance and steppe bird population productivity – being higher in years with more voles – could work in steppe grasslands analogously to the well-established relationship in the Arctic tundra between shorebirds and lemmings (e.g. Meltofte *et al.* 2007, Aharon-Rotman *et al.* 2014, Mckinnon *et al.* 2014). Moreover, recently recognized fading out in periodicity and abundances of voles across temperate Europe (Bierman *et al.* 2006, Cornulier *et al.* 2013) could be present also further east and could negatively influence the breeding performance of steppe birds at much larger scale. We encourage further studies to carry out the closer investigation of this relationship.

Start of the incubation was on average a bit earlier in terns than in shorebirds indicating that shorebirds could seek for the "protective umbrella" of terns – aggressive nest defenders (Whittam & Leonard 2000, del Hoyo *et al.* 2017). However, this state is only indicative,

because even on the first visits of breeding colonies, we found already depredated nests and we cannot rule out the possibility that some of the nests found during first visits were already replacement clutches. On other visits several days later, we found regularly new nests of terns as well as shorebirds so that whole colonies were very dynamic with fast changes of nests numbers and positions.

Nevertheless, such breeding "protective umbrella" was not effective in our study system and even in Common Terns 91% of the nests were depredated. Thus this pattern does not fit well into the long-standing perception of breeding under the "protective umbrella" of aggressive species as a successful breeding strategy (Quinn & Ueta 2008, Colwell 2010). To test this specifically, we would need a control representing shorebirds breeding out of terns and shorebird colonies, which would be challenging and difficult given the more or less pronounced "colonial breeding nature" of all focus species (Cramp & Simmons 1983, del Hoyo *et al.* 2017). The best candidate species could be Little Ringed Plover, which is not itself an active defender contrary to Northern Lapwing (Elliot 1985, Kis *et al.* 2000). When examining a higher number of breeding associations with terns and without terns, at least direct effect of terns could be assessed. Contrary to our expectation, nest predation was more intense on islands in comparison with the banks of the lakes which were more accessible for potential predators. However, the pattern can be driven by the low sample size of island shorebirds nests in our case.

Our sampling period corresponds with the beginning of the breeding season for all seven shorebirds species in the given region and egg measurements are in good concordance with already published information from former Soviet Union (Dement'ev & Gladkov 1969). Recorded interspecific nest scrape reuse when Black-winged Pratincole took over the vacant (predated) nest scrape of Black-winged Stilt has not been so far reported and it is in line with the prevalence of such behaviour under colonial breeding conditions and the close proximity of several breeding shorebirds species (Kubelka *et al.* 2014). The nest scrape would not be vacant for Black-winged Pratincole without fast depredation of the Black-winged Stilt clutch indicating that high nest predation could increase availability of vacant nest scrapes and promote nest scrape reuse behaviour.

The main limitations of our study are the short period of data collection and rather smaller sample sizes. The year 2017 could be exceptionally bad in terms of nest predation and without data from more seasons we cannot rule this possibility out. Moreover, we covered only the start of the breeding season which may experience higher nest predation rates comparing to the later part of the breeding season, similarly to findings in European agricultural landscape (Kubelka & Šálek 2013), at European coastline (Pienkowski 1984), in temperate North America (Alberico *et al.* 1991) or in the Arctic (Reneerkens *et al.* 2016). However, no significant seasonal differences in nest predation or even opposite trends were also reported (Dyrcz *et al.* 1981, Ottvall 2005, MacDonald & Bolton 2008, Kosztolányi *et al.* 2009, Weiser *et al.* 2017). Therefore, more extensive datasets covering a whole breeding season in Astrakhan region are needed. Given this persisting geographical knowledge gap, we encourage researchers to focus on shorebirds nest success and other demographic parameters monitoring in the central part of the Eurasian continent where apart from predation, bird

populations are currently facing negative agriculture practice changes in the steppe habitat (Kamp *et al.* 2011).

Our findings suggest that associations of breeding shorebirds in steppe landscape in the temperate region could recently suffer high nest predation rates with possible negative consequences for species population dynamics. Whether our study is an exception or whether it fits into the broader pattern of nest predation in Eurasian steppes remains to be investigated.

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Fig. 1. Location of the study area in steppe landscape of Astrakhan region, Russia.

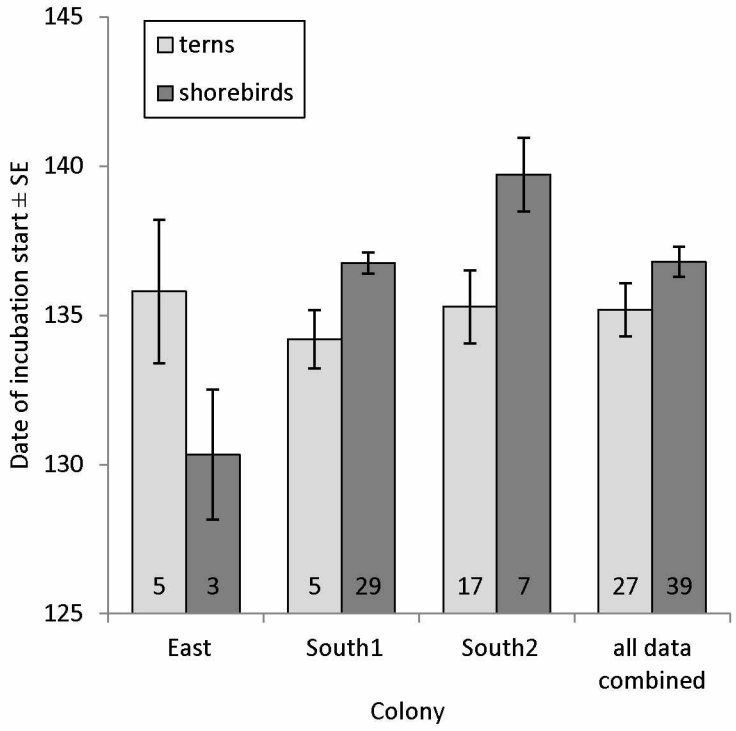

Fig. 2. Incubation start for nests of shorebirds (*Himantopus himantopus* n = 13 nest, *Recurvirostra avosetta* n = 12, *Glareola nordmanni* n = 10, *Charadrius alexandrinus* n = 3, *Vanellus vanellus* n = 1) and terns (*Sterna hirundo* n = 25, *Sternula albifrons* n = 2) in three breeding colonies near Promyslovka in Astrakhan region, Russia. Sample sizes in a number of nests are given in the base of the particular column.

Table 1. Description of five localities within the study area with shorebirds nests.

Locality	Habitat	GPS coordinates	Nr. of colonies	Nr. of species	Nr. of nests
Dam	fresh water marshland	46°42'53''N, 47°38'43''E	1	2	5
Promyslovka South	salt lake	45°39'05''N, 47°06'31''E	2	6	48
Liman	brackish/salt lake	45°45'23''N, 47°15'50''E	1	2	12
Lineynaya	fresh water lake	46°16'15''N, 47°28'48''E	1	4	12
Promyslovka East	salt lake	45°40'44''N, 47°12'59''E	1	1	3

Table 2. Clutch incubation start dates (e.g. 121 = 1st May, 151 = 31st May) and egg measurements (note that only beginning of the breeding season for all seven shorebirds species was covered).

Species	Incubation start			Egg length			Egg width			Nr. of eggs	Nr. of nests
	Mean	SD	Range	Mean	SD	Range	Mean	SD	Range		
Black-winged Pratincole *Glareola nordmanni*	139.2	4.0	129–145	31.97	1.23	29.2–34.2	24.70	0.89	22.8–26.4	61	25
Pied Avocet *Recurvirostra avosetta*	137.7	5.0	126–144	51.20	2.04	47.5–55.4	35.08	0.93	33.1–37.1	46	15
Black-winged Stilt *Himantopus himantopus*	136.8	2.7	131–145	43.77	1.95	39.0–48.0	31.1	1.12	28.5–33.5	107	29
Kentish Plover *Charadrius alexandrinus*	137.0	1.0	136–138	32.28	0.69	31.6–33.6	22.51	0.41	21.8–23.1	9	3
Little Ringed Plover *Charadrius dubius*	131.3	2.1	129–133	29.23	0.79	27.7–30.3	22.21	0.42	21.5–22.7	10	3
Northern Lapwing *Vanellus vanellus*	128.5	4.9	125–132	45.07	1.79	43.8–47.1	33.50	0.31	33.2–33.8	3	2
Common Redshank *Tringa totanus*	137.0	–	137	43.94	0.85	43.1–45.0	29.58	0.13	29.5–29.8	4	1

Table 3. Daily and total nest predation rates for seven shorebirds species.

Species	Daily nest predation	SE	Total nest predation (%)	Nr. of predated nests	Exposure (days)	Nr. of nests	Nr. of localities
Black-winged Pratincole *Glareola nordmanni*	0.140	0.046	95.8	8	57	14	4
Pied Avocet *Recurvirostra avosetta*	0.138	0.064	98.4	4	29	10	3
Black-winged Stilt *Himantopus himantopus*	0.084	0.027	91.2	9	107.5	26	3
Kentish Plover *Charadrius alexandrinus*	0.174	0.112	99.6	2	11.5	3	1
Little Ringed Plover *Charadrius dubius*	0.057	0.055	81.3	1	17.5	3	2
Northern Lapwing *Vanellus vanellus*	0.143	0.132	99.2	1	7	2	2
Common Redshank *Tringa totanus*	0	–	0	0	6	1	1

Table 4. Daily nest predation rates for five localities and two nest locations in shorebirds.

Locality	Daily nest predation	SE	Nr. of predated nests	Exposure (days)	Nr. of nests	Nr. of species
Dam	0.133	0.072	3	22.5	4	2
Promyslovka South	0.133	0.029	18	135	34	6
Liman	0.050	0.034	2	40	9	1
Lineynaya	0.063	0.043	2	32	9	4
Promyslovka East	0	–	0	6	3	1
Island nests	0.154	0.071	4	26	10	2
Mainland nests	0.100	0.021	21	209.5	49	7
All nests combined	0.106	0.020	25	235.5	59	7

Red-wattled Lapwing (*Vanellus indicus*) and Kentish Plover (*Charadrius alexandrinus*) with clutch, UAE 2018

Chapter 10

Review of inter and intraspecific predation among shorebirds

Vojtěch Kubelka

(manuscript)

Review of inter and intraspecific predation among shorebirds

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Shorebirds are generally perceived as predators of invertebrate prey, varying from insect, lumbricids to bivalves (e.g. Colwell, 2010; BirdLife International, 2018; del Hoyo *et al.*, 2018). However, particular occasions suggest that these gentle creatures can purposefully prey on other vertebrates, including eggs of other birds (e.g. Cramp & Simmons, 1983; Poole, 2015). In this review, I focus on specific cases, when one species of shorebirds predates on eggs or chicks of other shorebird species followed by the consummation of the prey.

I considered as shorebirds 245 species from 16 families classified into the order Charadriiformes (del Hoyo & Collar, 2014; Gill & Donsker, 2016; del Hoyo *et al.*, 2018). I excluded gulls, terns and auks for the better eco-morphological coherence of the focal species (del Hoyo *et al.*, 2018). I obtained the average adult body mass for each interacting species from Myhrvold *et al.*, (2015) and defined the species as non-aggressive or aggressive against potential predators (actively attacking them) during incubation or chick-rearing period according to Larsen *et al.*, (1996) with use of current information (del Hoyo *et al.*, 2018) and primary literature for some species. Situations, when shorebird females can just kill a chick from another family at the border of family foraging ranges in lapwings or godwits (Byrkjedal *et al.*, 2000; Teunissen *et al.*, 2008) or reported destroying eggs and infanticide among parents in several species of Jacanas (D. A. Jenni in Stephens, 1982; Emlen *et al.*, 1989; Chen *et al.*, 2008) where victims were not consumed, were omitted from this review.

From primary literature or personal communication, I was able to obtain 14 cases of interspecific predation relationships and two cases of intraspecific predation among shorebirds, altogether involving 11 species of predators and 13 species of prey (table 1). Regarding all 16 interactions, predator species had on average bigger body mass: 290 g ± 56 (SE) than prey species of shorebirds: 172 g ± 47 (SE) and they differed significantly (paired Wilcoxon signed rank test; $P = 0.014$). In all 16 interactions, predator shorebirds were always regarded as aggressive species against potential predators during breeding (100%), whereas prey shorebirds were defined as aggressive ones only in 50% of cases.

Table 1. Inter and intraspecific predation among shorebirds. Species are ordered according to IOC Word Bird List, ver. 6.3 (Gill & Donsker, 2016). Notes: [1]Country was assumed from the context (Cramp & Simmons, 1983); [2]Not directly observed but Snowy Sheathbills were only possible predators (Jones, 1963); [3]The chick was probably already dead (Marks et al., 2002); "at least 1" = context indicated more than one case possible, but it was not explicitly stated.

Predator species	Prey species	Prey items	N of cases	Where	References
Eurasian Thick-knee *Burhinus oedicnemus*	Northern Lapwing *Vanellus vanellus*	eggs	1	France[1]	Cramp & Simmons 1983
Great Thick-nee *Esacus recurvirostris*	Kentish Plover *Charadrius alexandrius*	eggs	1	India	Dharmakurmarsinhji in Ali & Ripley 1981
Snowy Sheathbill *Chionis albus*	Snowy Sheathbill *Chionis albus*	eggs[2]	regularly	Antarctica	Jones 1963
Eurasian Oystercatcher *Haematopus ostralegus*	Northern Lapwing *Vanellus vanellus*	eggs	1	Netherlands	Teunissen *et al.* 2008
Spur-winged Lapwing *Vanellus spinosus*	Black-winged Stilt *Himantopus himantopus*	eggs	1	Greece	E. Makrigianni *in litt.*
Red-wattled Lapwing *Vanellus indicus*	Kentish Plover *Charadrius alexandrius*	eggs	1	UAE	Kosztolányi *et al.* 2009
Blacksmith Lapwing *Vanellus armatus*	Kittlitz's Plover *Charadrius pecuarius*	chick	1	South Africa	Calf 2002
Blacksmith Lapwing *Vanellus armatus*	White-fronted Plover *Charadrius marginatus*	eggs	at least 1	South Africa	Wiersma *et al.* 2018
Black-tailed Godwit *Limosa limosa*	Northern Lapwing *Vanellus vanellus*	eggs	1	Netherlands	Teunissen *et al.* 2008
Bristle-thighed Curlew *Numenius tahitiesis*	Grey Plover *Pluvialis squatarola*	chick[3]	1	Alaska	C. Babcocks in Marks *et al.* 2002
Ruddy Turnstone *Arenaria interpres*	Eurasian Oystercatcher *Haematopus ostralegus*	eggs	at least 1	Finland	Brearey & Hildén 1985
Ruddy Turnstone *Arenaria interpres*	Common Redshank Tringa totanus	eggs	at least 1	Finland	Brearey & Hildén 1985
Ruddy Turnstone *Arenaria interpres*	Spotted Sandpiper *Actitis macularia*	eggs	regularly	USA	Alberico *et al.* 1991
Ruddy Turnstone *Arenaria interpres*	Ruddy Turnstone *Arenaria interpres*	eggs	1	Finland	Vuolanto 1968
Ruddy Turnstone *Arenaria interpres*	Temminck's Stint *Calidris temminckii*	eggs	at least 1	Finland	Rönka *et al.* 2006
Black Turnstone *Arenaria melanocephala*	Red-necked Phalarope *Phalaropus lobatus*	eggs	1	USA	Handel & Gill 2001

Turnstones

Both, Ruddy Turnstone (*Arenaria interpres*) and Black Turnstone (*Arenaria melanocephala*) are well known as opportunistic feeders with very diverse diet, containing also eggs of small ground-nesting birds (Cramp & Simmons, 1983; Handel & Gill, 2001). Therefore it is not surprising that Ruddy Turnstone is the most common species involved in predation among shorebirds (table 1). Ruddy Turnstone is known to predate and consume eggs of other water birds, namely several species of terns, gulls or ducks across locations ranging from Palearctic to North America and Pacific islands (Bergman, 1946; Crossin & Huber, 1970; Parkes *et al.*, 1971; Loftin & Sutton, 1979; Brearey & Hildén, 1985; Farraway *et al.*, 1986; Morris & Wiggins, 1986; Alberico *et al.*, 1991; Olson, 1996).

Sometimes it is not just an accidental predation, but turnstones can cause a large nest predation and damage issuing e.g. in the Royal Tern (*Thalasseus maximus*) colony abandonment in Florida (Loftin & Sutton, 1979) or depredate large proportion of Common Tern (*Sterna hirundo*) nests within a breeding colony in Toronto (Farraway *et al.*, 1986) or plunder gulls and terns colonies at Scandinavian islands (Brearey & Hildén, 1985). Nest depredation on Gray-backed Tern (*Sterna lunata*) nests by Ruddy Turnstones at Laysan Island in Pacific was so intense that Alexander Wetmore more than 90 years ago mentioned no chance for terns to breed until turnstones leave their wintering grounds (Olson, 1996).

Ruddy Turnstones were also responsible for a big proportion of eggs loses in Spotted Sandpiper (*Actitis macularia*) population breeding near to Common Tern colony in Leech Lake in Minnesota (Alberico *et al.*, 1991) and they are perceived as important nest predators for Temminck's Stint (*Calidris temminckii*) in Finland too (Rönkä *et al.*, 2006). Ruddy Turnstones can also occasionally predate nests of conspecifics as it was recorded at least once in Finland (Vuolanto, 1968).

Turnstones are not only capable to exploit unguarded nests, but they can purposefully attack incubating birds in pursuit of eggs. A quite dramatic story includes Ruddy Turnstones drugging the egg from beneath an incubating adult of Gray-backed Tern and devouring it directly next to the nest and pair of robbed terns (A. Wetmore in Bent 1929). Another narrative describes a situation when a group of Ruddy Turnstones attacked the nest of Sooty Tern (*Sterna fuscata*) and despite aggressive defence by parents, they reached and pecked the egg, which was later abandoned and left for the possible consummation by turnstones (Crossin & Huber, 1970). Also, Black Turnstone can be very aggressive and adults were observed to jabbing bill at incubating Red-necked Phalarope (*Phalaropus lobatus*) which eventually fled and turnstones got the eggs (Handel & Gill, 2001).

Strong, short and pointed bill of turnstones represents a clear advantage for egg consummation because these birds are able to open even albatross eggs (Marks & Hall, 1992). Indeed, the egg-opening ability is important, otherwise, probably more species of shorebirds would occasionally incorporate energetically rich bird eggs into their diet. For example, Sanderlings (*Calidris alba*) were observed feeding on the Royal Tern eggs, but together with Ruddy Turnstones, which were probably responsible for eggs opening (Loftin & Sutton, 1979).

Egg predation behaviour in Ruddy Turnstone is probably spread by learning and watching other conspecific individuals opening eggs (Brearey & Hildén, 1985), therefore this behaviour can be so patchy and unpredictable among turnstones (Loftin & Sutton, 1979; Brearey & Hildén, 1985; Farraway *et al.*, 1986). Because high feeding specializations among individual Ruddy Turnstones is possible (Whitfield, 1990), it is probable that effective individuals can play an important role in spreading of egg predation behaviour among groups of turnstones.

Generally, turnstones are not perceived as predators from gulls and many terns (Brearey & Hildén, 1985; Farraway *et al.*, 1986), therefore they can be so successful egg predators (Brearey & Hildén, 1985), occasionally causing large damage to breeding colonies of terns and gulls (Loftin & Sutton, 1979; Brearey & Hildén, 1985; Farraway *et al.*, 1986; Olson, 1996). More likely, rather than a new phenomenon, suggested by (Brearey & Hildén, 1985), egg predation by turnstones is so scarce and regionally limited that the selection on perceiving turnstones as egg predators had not been strong enough to evolve adequate aggressive anti-predatory response in larids, often successfully performed against other avian predators (e.g. Cramp & Simmons, 1983; Quinn & Ueta, 2008; Sládeček *et al.*, 2014). However, some tern species were observed to attack turnstones near their nests (Crossin & Huber, 1970; Loftin & Sutton, 1979; Brearey & Hildén, 1985), which suggest probably more intense predator pressure from turnstones on terns in evolutionary time.

Curlews and Godwit

Bristle-thighed Curlew (*Numenius tahitiesis*) on its wintering grounds at Pacific islands is well known for eating eggs of many seabirds including terns, boobies, noddies, shearwaters, petrels or frigatebirds (Ely & Clapp, 1973; Marks & Hall, 1992; Olson, 1996). Exceptionally among shorebirds, Bristle-thighed Curlew can also use small stones for opening big albatross eggs (Marks & Hall, 1992). Once the Bristle-thighed Curlew tried to swallow Black-bellied Plover (*Pluvialis squatarola*) chick regurgitated by a gull in Alaska (C. Babcock in Marks et al., 2002). In the completely different environment of archipelagos in the middle of Pacific, though not directly confirmed, Bristle-thighed Curlews were likely responsible for egg predation in some nests of Tuamotu Sandpiper (*Prosobonia parvirostris*) at Tahanea atoll (D. Lank in litt.).

Bristle-thighed Curlews and Ruddy Turnstones are suggested to perform egg predation behaviour predominantly at occasions of other food shortage (Brearey & Hildén, 1985; Marks *et al.*, 2002) indicating opportunistic switch of prey or by a try-and-error independent invention of egg-eating behaviour during food shortage (Brearey & Hildén, 1985). Indeed, Bristle-thighed Curlews caused more intense depredation of seabird nests at Laysan Island in the Pacific during the first half of 20th century in the period when island vegetation was nearly eliminated by European Rabbits (*Oryctolagus cuniculus*), which must have reduced insect availability for curlews considerably, in comparison with the 1990s (Marks *et al.*, 2002).

Other curlews could be perhaps rare predators of other shorebirds as well, because diet of Eurasian Curlew (*Numenius arquata*) contains rarely also young birds and possibly eggs (Van Gils *et al.*, 2018) and Long-billed Curlew (*Numenius americanus*) was observed to

predate on eggs and nestlings of Horned Lark (*Eremophila alpestris*) in Canada (Sadler & Maher, 1976). Quite surprisingly, the invertebrate feeder, Black-tailed Godwit (*Limosa limosa*) was once recorded as the egg predator of Northern Lapwing (*Vanellus vanellus*) in the Netherlands (Teunissen *et al.*, 2008), indicating that under intensive video surveillance, unexpected predator and foraging behaviour can be recorded.

Lapwings and plovers

Lapwings are generally aggressive species (del Hoyo *et al.*, 2018) and three species were involved as predators in four predation interactions with other shorebirds (table 1). In the case of Blacksmith Lapwing (*Vanellus armatus*) predating on Kittlitz's Plover (*Charadrius pecuarius*) chick, the non-breeding foraging lapwing entered the plover's territory and despite distraction display from plovers, after five minutes of aggressive behaviour, lapwing found, pick up, shook to death and swallow one of two 2–3 days old plover chicks (Calf, 2002). Apart from presented interactions, Black-shouldered Lapwing (*Vanellus novaehollandiae*) is a suspected egg predator of Chatham Oystercatcher (*Haematopus chathamensis*) based on the close presence of lapwings near oystercatchers nests during video monitoring (Moore, 2014).

Pied Lapwing (*Hoploxypterus cayanus*) and Collared Plover (*Charadrius collaris*) were identified as predators of Sand-colored Nighthawk (*Chordeiles rupestris*) active nests at sand beaches of Peruvian rivers in Amazon rainforest (Menezes & Marini, 2017), which suggests that they could occasionally be a predator of shorebird's egg as well. Pacific Golden Plovers (*Pluvialis fulva*) were seen eating bird eggs on Laysan Island in the Pacific (Olson, 1996).

Other species

Thick-knees (Burhinidae) have a various diet with small portion regularly consisting of vertebrates as well, namely small amphibian and reptiles (del Hoyo *et al.*, 1996) but two species were recorded as exceptional predators of other shorebirds nests (table 1). The second case of intraspecific predation was reported for Snowy Sheathbill (*Chionis albus*) from islands near Antarctic peninsula. Only suspected predators for the missing eggs were the breeding birds themselves or other sheathbills (Jones, 1963). Sheathbills are omnivorous generalists, which is essential in the harsh environment of Antarctic and sub-Antarctic islands. Eggs and chick of other seabirds, especially penguins, represent an important part of sheathbills' diet (del Hoyo *et al.*, 1996), and other sheathbills, specifically non-breeders are assumed as principal eggs predators of conspecific (Jones, 1963). Intraspecific predation is also probable in Black-faced Sheathbill (*Chionis minor*) at Marion Island (Burger, 1979).

It was noted that Eurasian Oystercatcher (*Haematopus ostralegus*) can occasionally eat eggs and nestlings of other birds (Dement'ev & Gladkov, 1969), namely gulls and terns (Cramp & Simmons, 1983) or duck eggs (Jones, 2008), therefore it is expectable that they can rarely predate on other shorebirds nests as well (tab 1). Given the strong bill capable of egg-opening and the fact that several species of oystercatchers from Southern hemisphere are

understudied in comparison with North hemisphere relatives (Ens & Underhill, 2014), it is possible that also other species of oystercatchers can occasionally eat eggs of shorebirds.

Taken together, very diverse foraging tactics of shorebirds involve the eating of each other as well, though representing only a tiny proportion of the diet. Generally larger and more aggressive species of shorebirds are better predisposed to become eggs or chicks predators of other shorebirds. Only regular bird nests predators among shorebirds with regionally significant impact on reproductive output of prey species are turnstones. The pointed short bill represents a useful tool for egg-opening and the fact that turnstones are not often recognized by prey species as potential predators help them to predate effectively on bird eggs. The prevailing anecdotal nature of the evidence for predation behaviour among shorebirds and generally less known diet of tropical shorebirds suggest that such behaviour can be occasionally performed by more species, especially in the tropics and thus contribute to the already highly variable life history strategies of shorebirds.

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Eurasian Dotterel (*Eudromias morinellus*) with his clutch in Hardangervidda, Norway, 2008

Chapter 11

Global pattern of nest predation is disrupted by climate change in shorebirds

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(in revision)

Title: Global pattern of nest predation is disrupted by climate change in shorebirds

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Abstract: Ongoing climate change is thought to disrupt trophic relationships with consequences for interspecific interactions, yet the effects of climate change on species interactions are controversial and have not been estimated at a global scale. Using a unique database of 38,191 nests from 237 populations, we found that shorebirds have experienced a worldwide increase in nest predation over the last 70 years. Historically, there existed a latitudinal gradient in nest predation with the highest rates in the tropics, however, this pattern has been recently reversed in the Northern hemisphere most notably in the Arctic. This increased nest predation is consistent with climate-induced shifts in predator-prey relationships. Climatic events thus alter key predator-prey relationships that have global consequences for ecological communities and ecosystem processes via trophic interactions.

One Sentence Summary: Climate change increases offspring mortality in shorebirds that affects ecosystem processes worldwide via altered predator-prey interactions.

Main Text: Climate change is impacting on organisms at a global scale in several ways (*1–4*) including directly altering demographic parameters such as adult survival (*5*) and reproduction (*1*) or via altered trophic interactions such as mismatches between predators and prey (*1*, *6*, *7*). Successful recruitment is essential for balancing mortalities and maintaining viable populations, thus disruption of reproductive performance can have detrimental effects on wild populations (*8–10*). Alterations in demographic parameters are often attributed to recent climate change (*1*, *5*, *11*), especially in the Arctic, were the consequences of warming are expected to be pronounced (*6*, *12*). However, the evidence for impacts of climate change on species interactions is mixed, and to date there is no evidence of how such interactions are changing at a global scale (*1–3*).

Offspring mortality due to predation has a pivotal influence on reproduction performance of wild populations (*8*, *13–15*) and extreme rates of predation can quickly lead to species extinction (*16*). Thus nest predation represents a good indicator of reproductive performance in bird populations (*10*), and consequently, disruption to annual productivity through increased nest predation could have a detrimental effect on population dynamics that lead to increased extinction risks (*9*). Although predation is the most common cause of reproduction failure (*13*, *14*) and climate change has been proposed to influence predation (*12*), this important proposition has not been tested at a global scale.

To explore changes in spatial patterns of reproduction and the potential alterations in trophic interactions, we use nest predation data from shorebirds, a globally distributed group of ground-nesting birds that exhibit similarity in nest appearance and are exceptionally well-studied in the wild including ecology, behaviour and demography (*10*, *17*, *18*). We collected data from both published and unpublished sources that included 38,191 nests in 237 populations of 111 shorebirds species from 149 locations (fig. S1 and table S1) encompassing all continents across a 70-year time span. Here we use these data in a phylogenetic framework (*19*) to investigate changes in nest predation at unprecedented temporal and spatial scales.

Using our comprehensive dataset, here we show that rates of nest predation increased globally in the last 70 years. Daily nest predation, as well as total nest predation (reflecting the full incubation period for a given species), have increased overall worldwide since the 1950s' (Fig. 1, Fig. 2A, Fig. 2B and table S2). Thus the total nest predation was historically (until 1999) on average 43% ± 2% (SE) which has increased to 57% ± 2% since 2000. However, the extent of changes show considerable geographical variation: in the tropics and South temperate areas, the changes in daily and total nest predation were not significant, whereas in the North temperate zone, and especially the Arctic, the increase was pronounced (Fig. 1, Fig. 2A, Fig. 2B and table S2). This pattern holds across major clades of shorebirds (Fig. 2C, Fig. 2D and table S3). The pattern is also consistent with local changes since the daily and total nest predation has also increased significantly in well-monitored North temperate and Arctic breeding populations (Fig. 2E and Fig. 2F). Thus the total nest predation was historically 35% ± 6% that increased to 64% ± 5% in recent years (Fig. 2E, Fig. 2F, table S4 and table S5).

Life-history theory and regional empirical evidence predict that species that breed close to the Equator should exhibit higher rates of nest predation than species breeding in temperate and polar latitudes (*14*, *15*, *20*, *21*). Consistent with theoretical expectations, historic rates of nest predation in shorebirds follow the parabolic relationship between both daily and total rates of nest predation and latitude (Fig. 3 and table S6).

However, in recent years the daily nest predation changed only a modest extent in the tropics and Southern hemisphere (Fig. 3), although it increased nearly two-fold in the North temperate zone and three-fold in the Arctic compared with historic values (Fig. 2A, Fig. 2B and Fig. 3). Thus 70% of nests are now being depredated in the Arctic (Fig. 2B). As a consequence of latitude-dependent changes in nest predation, predation rates now increase from the equator to the Arctic, in contrast to the historic parabolic latitudinal pattern (Fig. 3 and table S6).

Climate change has been thought to influence trophic interactions (*1*, *6*, *7*, *12*), and to investigate whether altered rates of nest predation are driven by climate, we calculated the changes in ambient temperature in each shorebird population and tested whether the temperature changes predict the shifts in nest predation at a global scale (*19*). We used two proxies of climate change: the slope of annual mean temperature regressed over time; and the standard deviation of annual mean temperatures; these were measured over the time span of 30 years for each population. Indeed, higher rates in both the daily and the

total nest predation were associated with increased ambient temperatures and temperature oscillations (Fig. 4). Importantly, these results are robust to the choice of climatic variables over periods of 40 or 20 years (table S7).

Because predation is the most common cause of breeding failure (*13*, *14*), our results imply declining reproduction success in widely distributed bird group. This decline, unless compensated by higher juvenile or adult survival and/or increased production of clutches, will drive global population declines when recruitment is not sufficient to maintain existing population sizes (*9*, *10*). However, the evidence is mounting that adult survival of these long-distance migrants has recently decreased due to habitat loss at staging areas (*22*, *23*). Similarly, declining chick survival has been detected across Europe (*24*). Whereas tropical shorebirds may be able to increase the number of breeding attempts and thus compensate possible productivity loss, it is unlikely so at higher latitudes owing to short polar summers (*6*, *12*). Since most shorebirds are already declining (*18*, *23*, *25*), our results suggest that an important correlate of this decline could be higher rates of nest predation.

Temporal changes in nest predation were significant in the Northern hemisphere, particularly in the circumpolar Arctic and these changes were predicted by the extent of documented climate changes in areas of local populations. Mechanisms for this could work through climate change driven impacts on the abundance of alternative prey and interaction with predators (*1*, *6*, *12*). Lemmings, small rodents representing the key component of the Arctic food web, experienced a crash in their abundances and population cycling due to unsuitable snow cover resulting from ambient temperature increase and fluctuations (*26–28*). This change was documented over vast Arctic areas around the year 2000 (*26–28*) and the pattern was similar for temperate voles populations in Europe (*29*, *30*). These changes in rodent abundances led to extensive changes in predator-prey interactions in Northern hemisphere, where predators normally consuming rodents have to switch to alternative preys including shorebird eggs and thus increase the predation pressure on birds (*12*, *28*).

Demographic changes we report here have two major implications. First, migrating birds have been presumed to benefit from breeding in the Arctic thanks to the low predation pressure (*31*). Currently, however, the productivity of Arctic populations is declining due to high rates of nest predation, which means that the energy demanding long-distance migration to Nordic breeding grounds is no longer advantageous from nest predation perspective. Thus the Arctic now represents an extensive ecological trap (*32*) for migrating birds with a predicted negative impact on their global population dynamics. Second, Arctic birds are likely to suffer further declines in the future due to this synergistic effects of the climatically-driven increase of predation pressure at their breeding grounds, a trophic mismatch during chick rearing period (*6*, *33*), predicted shrinkage of suitable habitat (*6*, *12*) and deteriorated adult survival during migration (*22*, *23*). The future scientific challenge with crucial consequences for species conservation lies in disentangling effects of these drivers on the overall viability of bird species.

In conclusion, we have demonstrated that rapid alterations in species interactions took place at a global scale and that these changes correspond to altered climate. This underlines the need for understanding the effects of climate change not only for individuals and their populations, but also for interactions in complex ecosystems including preys and predators.

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Supplementary materials:

Materials and Methods

Figure S1

Tables S1 to S8

References (*1–222*)

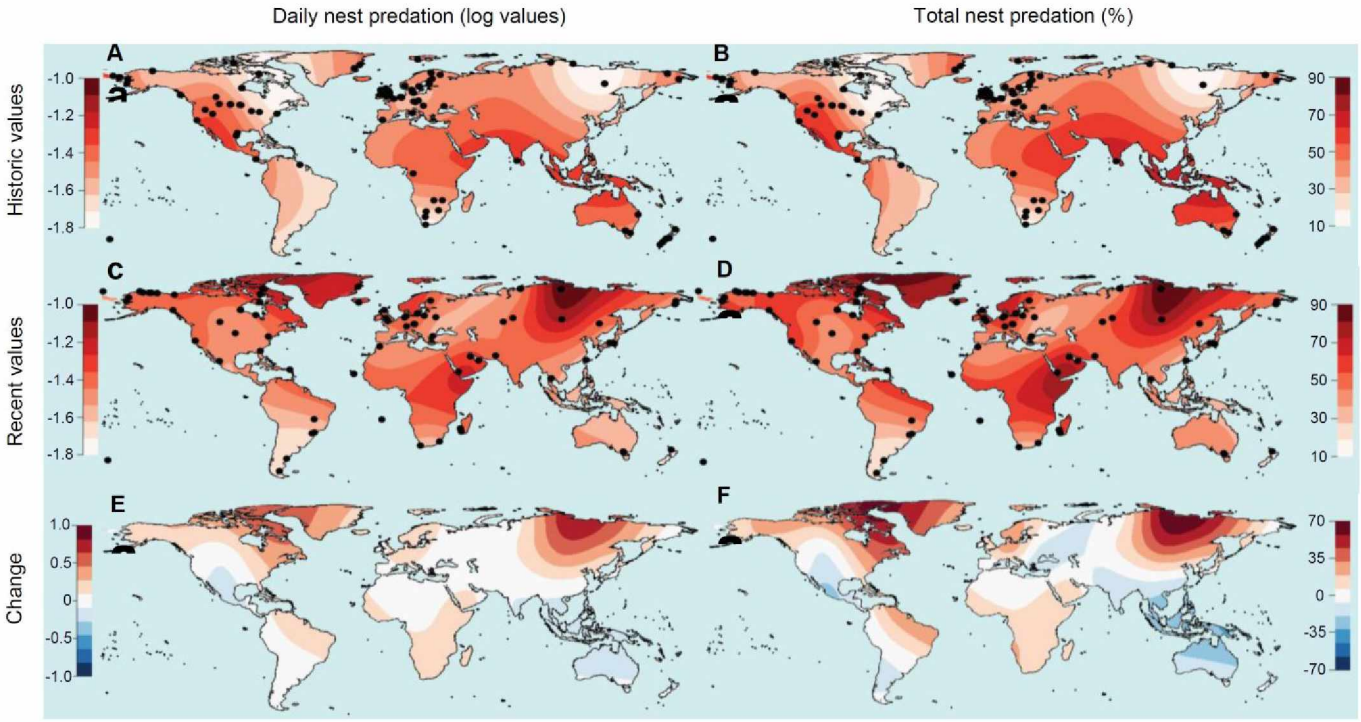

Fig. 1. Nest predation in shorebirds. (**A** and **B**) Historic rates of nest predation (1944–1999, 145 populations). (**C** and **D**) Recent rates of nest predation (2000–2016, 102 populations). (**E** and **F**) changes between historic and recent nest predation rates. (A, C, and E) Daily nest predation. (B, D and F) total nest predation. Dots show study locations, see (*19*) for details and fig. S1 for data distribution.

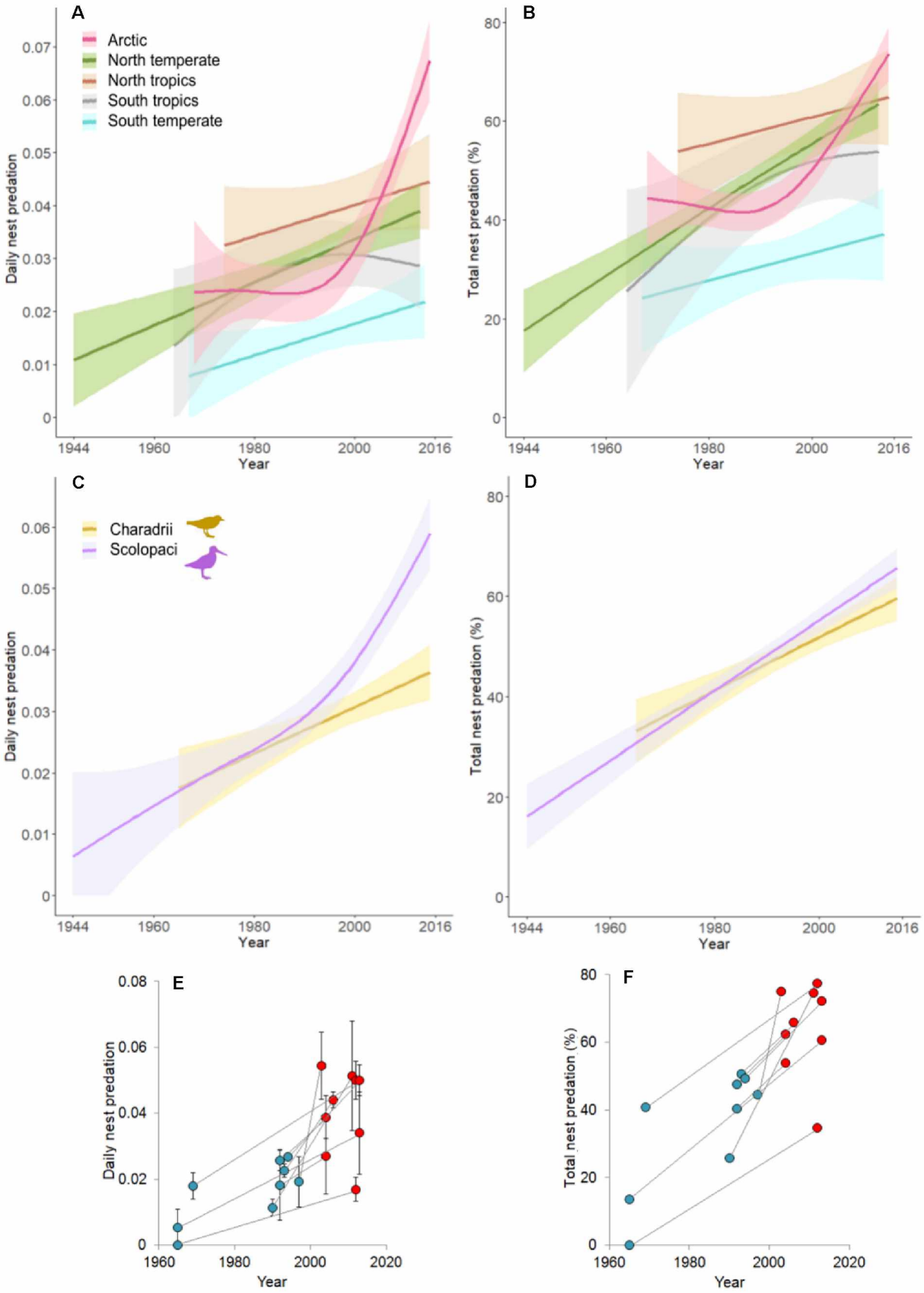

Fig. 2. Temporal changes in nest predation of shorebirds. (**A** and **B**) Nest predation rates for five latitudinal areas (Arctic n = 86 populations, North temperate n = 96 populations, North tropics n = 17 populations, South tropics n = 14 populations, South temperate n = 24 populations), see (*19*) for areas

definition and model description in table S2. (**C** and **D**) Nest predation rates for plovers and allies (Charadrii = 110 populations) and sandpipers and allies (Scolopaci = 127 populations), see (*19*) for clades definition and models description in table S3. (**E** and **F**) Local changes in nest predation rates for nine populations, each dot represents mean ± SE (E) over 2–19 breeding seasons for historic data (blue) and recent data (red), see table S4, see models description in table S5. (A–D) Generalized additive model fits with 95% confidence intervals. (A, C and E) Daily nest predation. (B, D and F) Total nest predation.

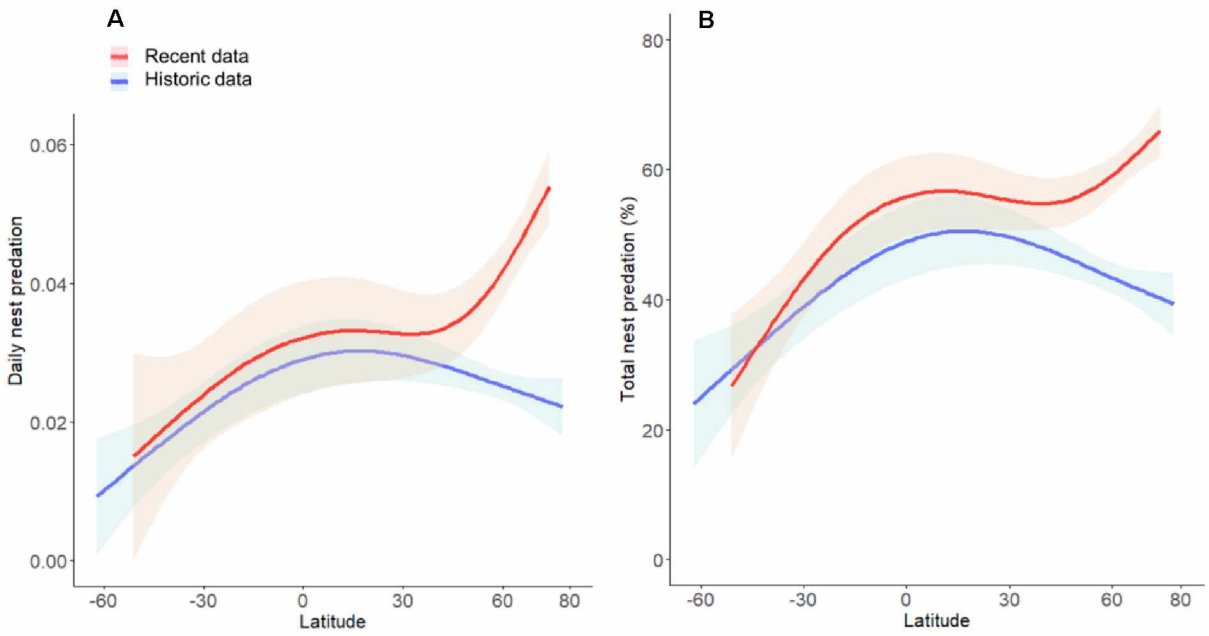

Fig. 3. Latitudinal gradient in historic versus recent nest predation of shorebirds. Daily (**A**) and total (**B**) nest predation rates (historic data before 2000, n = 145 populations; recent data after 2000, n = 102 populations), generalized additive model fits with 95% confidence intervals, see (*19*) for details and models description in table S6.

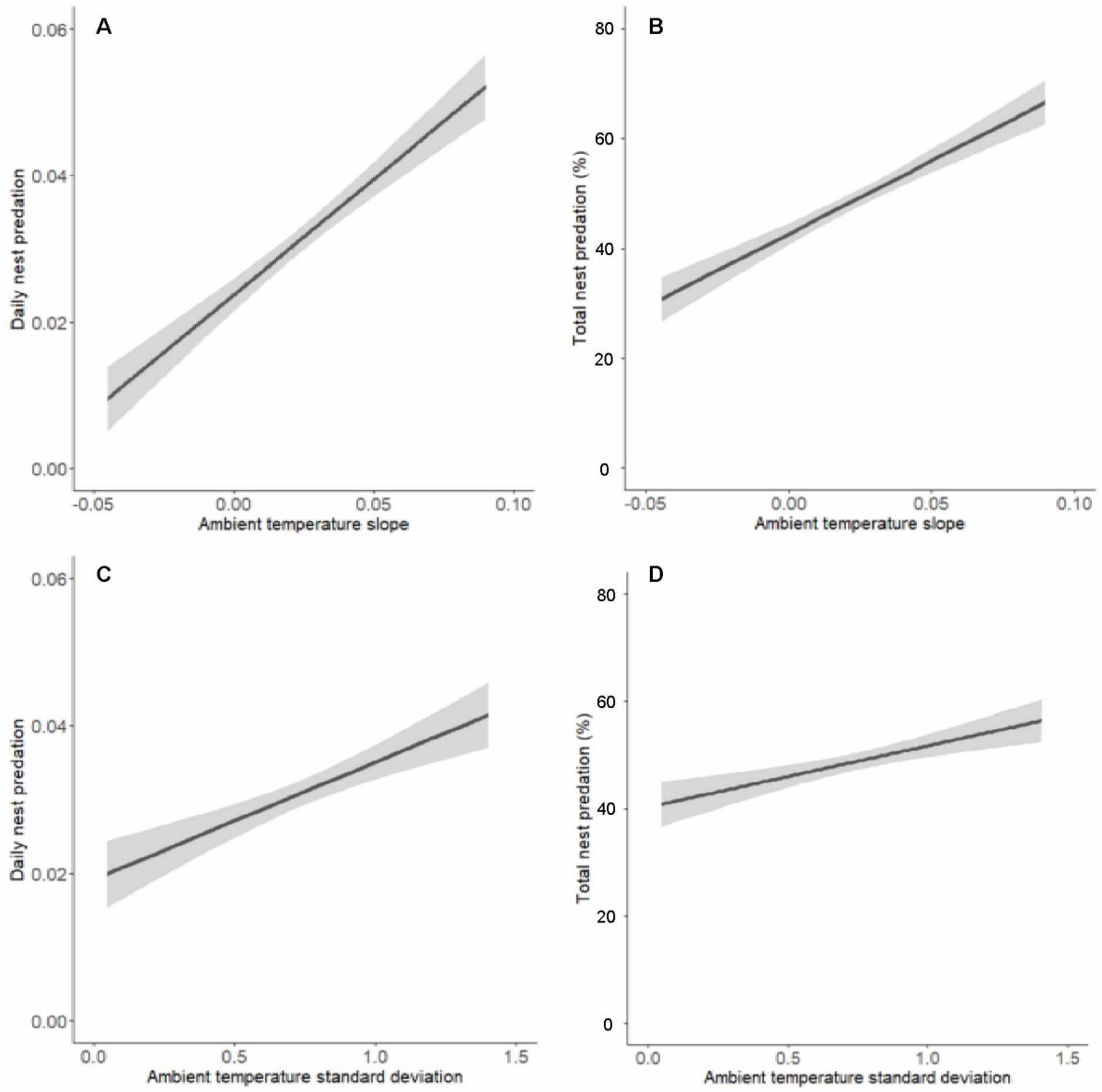

Fig. 4. Climate change effects on nest predation in shorebirds. (**A** and **B**) Relationship between daily (A) or total (B) nest predation rates and the slope of mean year temperatures. (**C** and **D**) Relationship between daily (C) or total (D) nest predation rates and the standard deviation of mean year temperatures. (A–D) Climatic data over 30 years prior to the last year of data collection, n = 247 population measurements, generalized additive model fits with 95% confidence intervals, see (*19*) for details and table S7 for models description.

Supplementary Materials for

Global pattern of nest predation is disrupted by climate change in shorebirds

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This PDF file includes:

Materials and methods

Data collection

We targeted search for data on nest predation in 245 shorebird species (*17*, *34*, *35*). Shorebirds (plovers, sandpipers and allies) are excellent study organisms for several reasons. First, many shorebirds are migratory encompassing several continents and they exhibit some of the best studied migratory behaviour in all organisms (*10*, *36–40*). Second, they have diverse reproductive strategies that have been used extensively to test evolutionary theories of life histories, sexual selection and adaptation (*41–44*). Third, shorebirds are ideal ecological indicator species of wetland habitats (*36*, *45–47*). The last, but not least, importantly from a conservation perspective, many shorebird species are declining (*18*, *23*, *25*) with some charismatic species facing to the imminent threat of extinction such as Spoon-billed Sandpiper (*48*) or Slender-billed Curlew (*Numenius tenuirostris*) (*49*). For the purpose of the comparative nest predation analyses it is essential that shorebirds i) are globally distributed; ii) have predominant ground nesting strategy and high inter-specific similarity in nest appearance to potential predators; iii) are sufficiently well-studied in terms of nest predation all over the world (*10*, *17*, *18*).

We searched articles using keywords (species Latin name + „breeding" or „breeding success" or „nest predation") in electronic databases including Web of Science, Searchable Ornithological Research Archive and Google Scholar, reference books (*50–56*), and reviews (*24*, *57*). We either downloaded articles from electronic databases or photocopied the printed version in the ornithological Alexander Library in Oxford (UK). Additionally, we asked members of International Wader Study Group for published grey literature and unpublished datasets concerning shorebirds nest predation. In total, these

searches provided over 12,000 articles. From these, we chose more than 900 papers for closer investigation and out of them, 143 publications held the information on nest predation or additional variables used in this study. Altogether, the final dataset contains nest predation for 38,191 nests (with continuous exposure of 503,120 days) in 237 populations of 111 shorebird species at 149 localities worldwide (fig. S1 and table S1).

For each shorebird population, we extracted 12 additional variables. We estimated latitude and longitude at the centre of the study area via GPS coordinates converter (www.gps-coordinates.net/gps-coordinates-converter) in decimal degrees format (three decimal spaces) with use of World Geodetic System 84 (WGS 84). We also recorded the year of the study (if the research was carried over more seasons, we used the mean) and the number of nests. The last eight variables represent a set of climatic factors addressing the climate change impact on species demographic parameters (*1*, *6*, *12*). Although it is possible that there is a small short-term advantage of warmer temperatures for the breeding productivity of birds at northern locations during particular breeding season (*12*, *58*), the larger the climate change over the years at a given location, the bigger negative impact on species and biotic interactions is expected (*3*, *6*, *59*).

Climatic variables

We extracted freely available ambient temperature data from the University of East Anglia Climate Research Unit database (CRU; http://www.cru.uea.ac.uk/,version3.10.01) (*60*). The CRU database is a global dataset containing interpolated monthly average temperatures from 1901 onward in a grid of spatial coordinates (0.5° × 0.5°). For each population, we selected temperatures from 40 years prior to the last year of data collection, inclusive and calculated mean year temperatures. We computed two main indices of climate change from those data: 1) the slope of the regression of mean year temperatures over 30 years prior to the last year of data collection, the higher positive slope, the more pronounced effect of climate change (global warming) was supposed; 2) the standard deviation of mean year temperatures over 30 years prior to the last year of data collection, the higher standard deviation, the more pronounced effect of climate change (climatic instability) was supposed. For the sensitivity control of the chosen period of 30 years, we prepared the same temperature slope and temperature standard deviation variables also for 40, 20 and 10 years prior to the last year of data collection, issuing in eight climatic variables for each population in total (table S7).

Data processing

We used two response variables in the study. Daily nest predation rate of nests according to Mayfield defined as the number of predated nests divided by the exposure of all nests in days (*61*, *62*) or follow-up methods (*63–65*) was the target variable for the nest predation rate, standardized among species and locations (*14*). We calculated the standard error for each data point following Johnson (*65*). We computed total nest predation rate of the nests as $1-((1-\text{daily nest predation rate})^{\text{incubation period}})$, where incubation period means the egg-laying and incubation period in days together for particular species (*61*, *62*). Since egg-laying and incubation period represent the interval for which the successful nest with eggs is exposed to potential predators, the total nest predation rate gives species-specific nest predation rate (mean percentage of nests being depredated in particular population) with respect to species life-history strategies (*20*, *66*). Total nest predation rate can be well used for inspecting spatial patterns because species are geographically restricted and their incubation period is also connected with the particular location. However, we must interpret temporal patterns in total nest predation rate with increased caution,

because changes in sampled species composition (with different incubation period) over the years has no ecologically relevant nature and albeit having probably only limited influence, species composition could affect average total nest predation rate for a particular period. Egg-laying and incubation period was the same for every population of particular species, obtained from Myhrvold (*67*) or from primary articles. Where not available (six cases), we expected egg-laying periods to be identical with values in closely related species. We refer to these variables through the article as daily nest predation and total nest predation, the later expressed between 0–100%.

For 97 populations (41%), daily nest predation or exposure in days and number of depredated nests were given in the source data. Daily nest predation was in the particular article: 1) directly given; 2) computed from the given exposure and number of predated nests; 3) computed as a mean weighted by sample size (number of nests) from daily nest predation values available for particular habitats, treatments etc.; 4) back-calculated from total nest predation provided by authors with the period for which the total nest predation was extrapolated; or 5) obtained by combination of aforementioned approaches.

The procedure of computing the exposure for daily nest predation is defined as follows. The exposure for hatched nests is from a day of finding until known or predicted hatching (e.g. 11 April and 28 April means 28-11 = 17 days of exposure). The exposure for depredated nests is from day of finding until midpoint assumption between last positive and first negative visits of the particular nest, the exposure for failed nests due to any other reason than predation (agriculture machinery, flooding, trampling etc.) or for nest with an unidentified fate is from day of finding until the last positive visits (not midpoint assumption between last positive and first negative visits of the nest).

For 140 populations (59%), daily nest predation and the total exposure were not provided but numbers of nests hatched, predated or failed for other reasons were reported instead for "apparent predation" or "apparent survival" computation (*61*, *62*, *68*). Therefore we used the Beintema's method (*69*) for estimating the exposure for these nests to be subsequently able to convert "apparent predation" to daily nest predation values. The logic of the method is that average successful nest is found halfway from laying to hatching (e.g. 15 days) and the depredated nest is lost halfway from this 15-days period. However, if most nests were found earlier after egg-laying, mean observation time set up on 0.5 of egg-laying and incubation period needs to be adjusted (*69*). We applied two additional options of mean observation time (0.9 and 0.6) to account for this. The first option was used for studies, where authors were checking the study plot for new nests every day and where most nests were found during the egg-laying period. The second option was applied for the majority of cases, where study plots were checked for new nests once or twice per week and most of the nests were found before reaching the half of incubation stage. The default 0.5 option was employed when data from nest card schemes were analysed or visits of the locality were very scarce and thus the incubation stage of found nest was random.

To check the correctness of our approach, we plotted computed daily nest predation rates against given ones in 56 shorebird populations for which both approaches were available. The computed daily nest predation highly correlated with given values: Pearson's correlation coefficient, $r_s = 0.96$, $P < 0.001$, mean daily nest predation computed value = 0.042 ± 0.004(SE), given value = 0.046 ± 0.005(SE), pairs of values did not differ (paired t-test, $t = 1.70$, $df = 55$, $P = 0.094$) and temporal trends were consistent between groups of data with directly given daily nest predation and data where daily nest predation was derived from "apparent predation" (table S3), therefore all data were treated together.

Every nest where at least one chick hatched was regarded as successful. Only complete nest depredations were included in the predated nests category (partial egg loss were omitted). Clutches with unfertile eggs with present parents which had not been depredated over expected egg-laying and

incubation period were regarded as successful ones for the purpose of predation analyses. Nests with unclear fate (without any certainly survived period between two visits) were totally excluded from further computations and they are not included in sample sizes. In two cases, a single study from Antarctica (*70*) and a single study from Alaska (*71*), we presumed all failed nests being depredated, although it was not explicitly stated in the article. Potential small overestimation of predation in these cases should not present an issue because it goes against our assumptions of lower nest predation in polar regions (*14*, *20*, *72*).

Different populations of one species were defined as localities at least 40 km from each other. Southern hemisphere breeding season over two calendar years was attributed only to one year (the first one) to be comparable with the Northern hemisphere. When data were available for more seasons in particular population, the sum of depredated nests and overall exposure were pooled over years to obtain mean predation values with presenting the mean year of data collection.

The number of seasons involved in each data point varied from one to 44 years, mean = 5.3 ± 5.8 (SD), median = 3 years. Total exposure per data point varied between 77–70,000 days, mean = 2,123 ±6,508 (SD), median = 631 days. Number of nests varied between 12–5,000 nests, mean = 161 ± 479 (SD), median = 51 nests. Studies with fewer than 12 nests with known fate were omitted from all analyses as well as nests covered with cages in predator control management. We accounted for the number of nests per population in modelling (see Statistical analyses for details).

Where the fate was given for individual eggs only but not for whole nests and authors were not able to provide us with additional information, we omitted these data because such data are not possible to use for correct calculation of daily nest predation values for nests as the unit.

Data division

For the purpose of more detailed analyses of temporal trend in nest predation, we divided the whole data set into 1) five latitudinal areas: South temperate (from -62° to -30°) – 24 populations, South tropics (from -30° to 0°) – 14 populations, North tropics (from 0° to 30°) – 17 populations, North temperate (from 30° to 60°) – 96 populations and the Arctic (from 60° to 78°) – 86 populations; 2) two clades of shorebirds i) Charadrii – 110 populations (families: Charadriidae, Haematopodiae, Recurvirostridae, Burhinidae, Chionidae) and ii) Scolopaci and allies – 127 populations (families: Scolopacidae, Jacanidae, Glareolidae, Rostratulidae). For more detailed spatial pattern investigation we divided our dataset into the two subsets of historic and recent data (before and after the year 2000 – the year 2000 is in the latter period). The extensive change of Arctic and North temperate ecosystem food-webs, the crash of small rodent (lemmings and voles) population cycles and abundances dated around the year 2000 (*26–30*) led us to the assumption that this change could cause the increase in shorebirds nest predation via altered trophic interactions (*1*, *6*), because shorebirds nests are known as alternative prey instead rodents (*12*, *73*). Ten populations with long surveillance over decades and over the year 2000 were divided into two subsets. Nine of them with data from two and more seasons in a given period are described in table S4 and were used for pairwise comparison of historic and recent nest predation values at same localities for the same species (Fig. 2E, Fig. 2F, table S5). Otherwise, every population was classified into the historic or recent period (before or after 2000) according to the mean year of data collection, altogether accounting for 145 populations before 2000 and 102 populations after 2000 (Fig. 3). Further division according to shorebirds clades was not possible due to insufficient samples in some latitudinal areas and total lack of Scolopaci clade nest predation values from Southern hemisphere after the year 2000.

Maps and figures preparation

Values of daily nest predation which were log transformed after the addition of a small quantity (0.01) and original total nest predation values were used for extrapolation of nest predation over the globe (Fig. 1). A single data point from Antarctica (*70*) from the mean year 1988, daily nest predation = 0.0098, total nest predation = 27%, although included in all analyses, was not included in all maps (Fig. 1), to avoid non-appropriate extrapolation of nest predation over the whole continent of Antarctica. For all populations and their localities see fig. S1. Mapped nest predation rates were generated by generalized additive models (maximum dimension of the basis k = 50), with Gaussian error family (*74–76*) in R (ver. 3.3.3) (*77*) for each point on the globe using latitude/longitude and known daily and total nest predation values separately. Daily nest predation values, as well as total nest predation values in maps, were presented in nine colour categories. The scale was the same for historic and recent values. Differences between historic and recent values were plotted for the figures of change in daily and total nest predation at the scale of 11 colour categories (Fig. 1E and Fig. 1F) with use of R (ver. 3.3.3) (*77*). Figures 2A-D, 3A, 3B, 4A and 4D were generated by the generalized additive model of the given relationship with 95% confidence intervals, the dimension of the basis (k) = 5, Gaussian error family (*74*) and plotted with 'ggplot' function in 'ggplot2' R package (*78*).

Statistical analysis

All statistical analyses were performed with R (ver. 3.3.3) (*77*). To assure normality of response variables, all daily nest predation values were adjusted to original value + 0.01 and log-transformed before entering analyses, total nest predation values were left in their original form. For the most of analyses, we used phylogenetically and spatially controlled generalized linear models. Specifically, we control for 1) phylogeny – we obtained species level of phylogeny from current avian tree (*79*) with manual addition of two recently recognized species: Snowy Plover (*Charadrius nivosus*) (*80*) and Wilson's Snipe (*Gallinago delicata*) (*17*, *35*). We created a variance–covariance matrix that is defined by the phylogeny (*81–83*) and incorporated it into each model. Because data were analysed on the population level, we accounted for this by incorporating the random effect of the species into each model; 2) spatial autocorrelation – we created a spatial matrix from GPS coordinates of each locality for each population following established approach (*83*, *84*) and incorporated it into each model; 3) number of nests – due to the fact that nest predation values obtained from smaller sample of nests could be less precise (*69*), we accounted for this in two ways: i) incorporating control variable, the logarithm of number of nest into each model and ii) creating diagonal matrix from number of nests (*74*) and incorporating it into each model. Due to the fact that two explanatory climatic factors and other possible explanatory variables were inter-correlated (see correlation matrix in table S8), we performed the climatic modelling in the sequence of simple linear mixed-effects kinship models (table S7) with control for phylogeny, spatial autocorrelation and sample size (see above). Only for within-population temporal variation in predation (table S5), we used linear mixed-effect models (*74*) with random effects of species and locality. Phylo-spatial models were fitted using the the package 'coxme' (*85*). Linear mixed-effects models were fitted with the 'lme4' package (*86*). Residuals from all tests were checked for normality in quantile-quantile plot (*74*). All statistical tests were two-tailed.

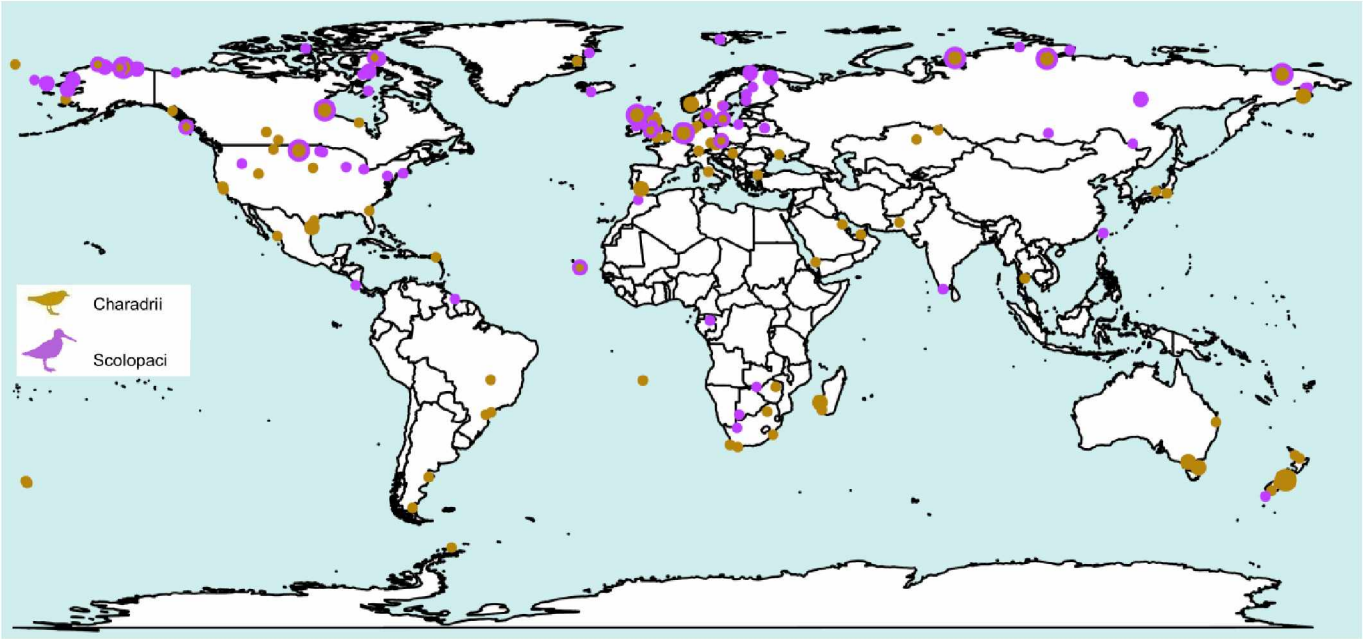

Fig. S1. Geographical distribution of the analysed data on nest predation of shorebirds. Alltogether, 237 populations of 111 shorebirds species at 149 localities were used in analyses. Dots of locations are divided into three size categories (small = 1 population only, medium = 2–3 populations, big = 4 and more populations per locality). Where shorebirds from both clades were studied, dots are presented in both colours.

Table S1. Shorebird species used in the study with number of populations and relevant data sources.

Species order	Species	N populations	Data sources
1	Eurasian Thick-knee (*Burhinus oedicnemus*)	2	(Taylor 2006) (*87*), (Nadeem *et al.* 2014) (*88*), Nadeem in litt.
2	Water Thick-knee (*Burhinus vermiculatus*)	1	(Dobson 2004) (*89*)
3	Snowy Sheatbill (*Chionis albus*)	1	(Favero 1993) (*70*)
4	Magellanic Plover (*Pluvianellus socialis*)	1	(Lishman & Nol 2012) (*90*), C. Lishman in litt.
5	American Black Oystercatcher (*Haematopus bachmani*)	1	(Tessler & Garding 2006) (*91*)
6	American Oystercatcher (*Haematopus palliatus*)	2	(Sabine *et al.* 2005) (*92*), (Barbieri & Delchiaro 2009) (*93*)
7	African Oystercatcher (*Haematopus moquini*)	2	(Calf & Underhill 2002) (*94*), (Scott *et al.* 2011) (*95*)
8	Eurasian Oystercatcher (*Haematopus ostralegus*)	5	(Hughey 1985) (*96*), (Beintema & Müskens 1987) (*97*), (Rudenko 1998) (*98*), (Jackson & Green 2000) (*99*), (Otwall 2005) (*100*)
9	Pied Oystercatcher (*Haematopus longirostris*)	1	(Lauro & Nol 1995) (*101*)
10	Variable Oystercatcher (*Haematopus unicolor*)	1	(Michaux 2013) (*102*)
11	Chatham Oystercatcher (*Haematopus chathamensis*)	1	(Moore & Reid 2009) (*103*)
12	Sooty Oystercatcher (*Haematopus fuliginosus*)	1	(Lauro & Nol 1995) (*101*)
13	Black-winged Stilt (*Himantopus himantopus*)	2	(Hughey 1985) (*96*), (Cuervo 2003) (*104*)
14	Black Stilt (*Himantopus novaezelandiae*)	1	(Pierce 1986) (*105*)
15	Pied Avocet (*Recurvirostra avosetta*)	2	(Beintema & Müskens 1987) (*97*), (Cuervo 2003) (*104*)
16	American Avocet (*Recurvirostra americana*)	1	(Herring *et al.* 2011) (*106*)
17	Northern Lapwing (*Vanellus vanellus*)	16	(Bain 1987) (*107*), (Beintema & Müskens 1987) (*97*), (Galbraith 1988) (*108*), (Baines 1990) (*109*), (Berg *et al.* 1992) (*110*), (Blomqvist & Johansson 1995) (*111*), (Flodin *et al.* 1995) (*112*), (Jackson & Green 2000) (*99*), (Hart *et al.* 2002) (*113*), (Schröpfer 2002) (*114*), (Šálek & Šmilauer 2002) (*115*), (Köster & Bruns 2003) (*116*), (Otwall 2005) (*100*), (Junker *et al.* 2006) (*117*), (Sharpe 2006) (*118*), (Kragten & De Snoo 2007) (*119*), (Pucha *et al.* 2009) (*120*), (Zámečník *et al.* 2017) (*121*), V. Kubelka unpublished data, M. Šálek unpublished data, V. Štorek in litt.
18	Spur-winged Lapwing (*Vanellus spinosus*)	1	(Makrigianni *et al.* 2008) (*122*), E. Makrigianni in litt.
19	Crowned Lapwing (*Vanellus coronatus*)	1	(Ade 1979) (*123*)
20	Grey-headed Lapwing (*Vanellus cinereus*)	1	(Takahashi & Ohkawara 2007) (*124*)
21	Black-shouldered Lapwing (*Vanellus novaehollandie*)	3	(Barlow *et al.* 1972) (*125*), (Giese & Jones 1996) (*126*), (Cardilini *et al.* 2013) (*127*)
22	Sociable Lapwing (*Vanellus gregarius*)	2	(Watson *et al.* 2006)(*128*), (Shedon *et al.* 2013) (*129*), P. Donald & I. Fisher in litt.
23	Southern Lapwing (*Vanellus chilensis*)	2	(Cerboncini *et al.* 2015) (*130*), (Santos & Macedo 2017) (*131*), R. A. Cerboncini in litt., E. S. A. Santos & R. H. Macedo in litt.
24	Wrybill (*Anarhynchus frontalis*)	1	(Hughey 1985) (*96*)
25	Golden Plover (*Pluvialis apricaria*)	1	(Byrkjedal 1987) (*132*)
26	Pacific Golden Plover (*Pluvialis fulva*)	3	(Schekkerman *et al.* 2004) (*133*), (Arctic Shorebird Demographics Network 2016) (*134*), P. Tomkovich unpublished data
27	American Golden Plover (*Pluvialis dominica*)	3	(Moitoret *et al.* 1996) (*71*), (Arctic Shorebird Demographics Network 2016) (*134*)
28	Grey Plover (*Pluvialis squatarola*)	4	(Kondratyev 1982) (*135*), (Moitoret *et al.* 1996) (*71*), (Tomkovich & Dondua 2011) (*136*), (Arctic Shorebird Demographics Network 2016) (*134*)
29	Northern Red-breasted Plover (*Charadrius aquilonius*)	1	(Wills *et al.* 2003) (*137*)
30	Common Ringed Plover (*Charadrius hiaticula*)	5	(Kondratyev 1982) (*135*), (Pienkowski 1984) (*138*), (Jackson & Green 2000) (*99*)
31	Semipalmated Plover (*Charadrius semipalmatus*)	2	(Jehl 1971) (*139*), (Cooper & Miller 1997) (*140*)
32	Long-billed Plover (*Charadrius placidus*)	1	(Katayama *et al.* 2010) (*141*)
33	Little Ringed Plover (*Charadrius dubius*)	2	(Dolanský & Žďárek 2001) (*142*), (Cepáková *et al.* 2007) (*143*), Cepáková *et al.* in litt.
34	Wilson's Plover (*Charadrius wilsonia*)	3	(Bergstrom 1982) (*144*), (Brown & Brindock 2011) (*145*)
35	Killdeer (*Charadrius vociferus*)	1	(Kantrud & Higgins 1992) (*146*)
36	Piping Plover (*Charadrius melodus*)	3	(Catlin *et al.* 2011) (*147*), (Richardson 1999) (*148*), (White 2005) (*149*)
37	Black-banded Plover (*Charadrius thoracicus*)	2	(Zefania *et al.* 2008) (*150*), C. Carmona *et al.* in litt., L. Eberhart-Phillips *et al.* in litt.
38	Kittlitz's Plover (*Charadrius pecuarius*)	1	C. Carmona *et al.* in litt., L. Eberhart-Phillips *et al.* in litt.
39	St Helena Plover (*Charadrius sanctaehelenae*)	1	(Burns et al. 2013) (*151*)
40	White-fronted Plover (*Charadrius marginatus*)	1	C. Carmona *et al.* in litt., L. Eberhart-Phillips *et al.* in litt.

Table continued on next page. Species are taxonomically ordered according to IOC Word Bird List (ver. 6.3, 2016) (*35*).

Table S1. Shorebird species used in the study with number of populations and relevant data sources. – table continued from the previous page.

Species order	Species	N populations	Data sources
41	Kentish Plover (*Charadrius alexandrinus*)	6	(Székely *et al.* 1994) (*152*), (Pietrelli *et al.* 2001) (*153*), (Kozstolány *et al.* 2009) (*154*), (Al Rashidi *et al.* 2011) (*155*), (Carmona-Isunza *et al.* 2015) (*156*), (Al Rashidi 2016) (*157*), M. C. Carmona-Isunza *et al.* in litt.
42	Snowy Plover (*Charadrius nivosus*)	5	(Paton 1994) (*158*), (Rupert 1997) (*159*), (Neuman 2003) (*160*), (Demers & Robinson-Nilsen 2012) (*161*), M. C. López in litt.
43	Red-capped Plover (*Charadrius ruficapillus*)	1	(Tan *et al.* 2015) (*162*)
44	Malay Plover (*Charadrius peronii*)	1	(Yasué *et al.* 2007) (*163*)
45	Two-banded Plover (*Charadrius falklandicus*)	1	G. D. Hevia & V. L. D'Amico in litt.
46	Double-banded Plover (*Charadrius bicinctus*)	2	(Hughey 1985) (*96*), (Keedwell & Sanders 2002) (*164*)
47	Lesser Sandplover (*Charadrius mongolus*)	1	P. Tomkovich unpublished data
48	Eurasian Dotterel (*Eudromias morinellus*)	1	(Byrkjedal 1987) (*132*)
49	Mountain Plover (*Charadrius montanus*)	1	(Dinsmore *et al.* 2002) (*63*)
50	Hooded Plover (*Thinornis cucullatus*)	2	(Dowling & Weston 1999) (*165*), (Baird & Daan 2003) (*166*)
51	Shore Plover (*Thinornis novaeseelandiae*)	1	(Davis 1994) (*167*)
52	Greater Painted-snipe (*Rostratula benghalensis*)	1	(Hsu & Severinghaus 2011) (*168*)
53	African Jacana (*Actophilornis africanus*)	1	(Tarboton 1992) (*169*)
54	Bronze-winged Jacana (*Metopidius indicus*)	1	(Butchart 2000) (*170*)
55	Northern Jacana (*Jacana spinosa*)	1	(Stephens 1984) (*171*), M. L. Stephens in litt.
56	Wattled Jacana (*Jacana jacana*)	1	(Osborne 1982) (*172*)
57	Eurasian Woodcock (*Scolopax rusticola*)	1	(Hoodles & Coulson 1998) (*173*)
58	American Woodcock (*Scolopax minor*)	1	(Miller & Jordan 2011) (*174*)
59	Auckland Snipe (*Coenocorypha aucklandica*)	1	(Miskelly 1990) (*175*)
60	Common Snipe (*Gallinago gallinago*)	3	(Beintema & Müskens 1987) (*97*), (Mongin 2002) (*176*), (Yarovikova 2003) (*177*)
61	Wilson's Snipe (*Gallinago delicata*)	1	(Kantrud & Higgins 1992) (*146*)
62	Short-billed Dowitcher (*Limnodromus griseus*)	1	(Arctic Shorebird Demographics Network 2016) (*134*)
63	Long-billed Dowitcher (*Limnodromus scolopaceus*)	4	(Kondratyev 1982) (*135*), (Moitoret *et al.* 1996) (*71*), (Arctic Shorebird Demographics Network 2016) (*134*)
64	Black-tailed Godwit (*Limosa limosa*)	3	(Beintema & Müskens 1987) (*97*), (Groen & Hemerik 2002) (*178*), (Groen *et al.* 2006) (*179*)
65	Hudsonian Godwit (*Limosa haemastica*)	1	(Jehl 1971) (*139*), (Arctic Shorebird Demographics Network 2016) (*134*)
66	Bar-tailed Godwit (*Limosa lapponica*)	1	(Larsen & Moldsvor 1992) (*180*)
67	Marbled Godwit (*Limosa fedoa*)	1	(Kantrud & Higgins 1992) (*146*)
68	Whimbrel (*Numenius phaeopus*)	5	(Jehl 1971) (*139*), (Skeel 1983) (*181*), (Larsen & Moldsvor 1992) (*180*), (Pulliainen & Saari 1993) (*182*), (Katrínardóttir *et al.* 2015) (*183*), (Arctic Shorebird Demographics Network 2016) (*134*), B. Katrínardóttir in litt.
69	Eurasian Curlew (*Numenius arquata*)	6	(Bain 1987) (*107*), (Berg 1992) (*184*), (Grant *et al.* 1999) (*185*), (Valkama *et al.* 1999) (*186*)
70	Far Eastern Curlew (*Numenius madagascariensis*)	1	(Antonov 2010) (*187*), A. I. Antonov in litt.
71	Long-billed Curlew (*Numenius americanus*)	1	(Redmond & Jenni 1986) (*188*)
72	Upland Sandpiper (*Bartramia longicauda*)	1	(Kantrud & Higgins 1992) (*146*)
73	Spotted Redshank (*Tringa erythropus*)	1	(Kondratyev 1982) (*135*)
74	Common Redshank (*Tringa totanus*)	4	(Beintema & Müskens 1987) (*97*), (Flodin *et al.* 1995) (*112*), (Jackson & Green 2000) (*99*), (Otwall 2005) (*100*)
75	Marsh Sandpiper (*Tringa stagnatilis*)	1	(Larionov 2015) (*189*)
76	Common Greenshank (*Tringa nebularia*)	1	(Christian & Hancock 2009) (*190*), M. Hancock in litt.
77	Wood Sandpiper (*Tringa glareola*)	2	(Pulliainen & Saari 1991) (*191*), (Larionov 2015) (*189*)
78	Willet (*Tringa semipalmata*)	1	(Kantrud & Higgins 1992) (*146*)
79	Terek Sandpiper (*Xenus cinereus*)	1	(Larionov 2015) (*189*)
80	Common Sandpiper (*Actitis hypoleucos*)	3	(Cuthbertson *et al.* 1952) (*192*), (Holland et al. 1982) (*193*), (Dolanský & Žďárek 2001) (*142*)

Table continued on next page. Species are taxonomically ordered according to IOC Word Bird List (ver. 6.3, 2016) (*35*).

Table S1. Shorebird species used in the study with number of populations and relevant data sources. – table continued from the previous page.

Species order	Species	N populations	Data sources
81	Spotted Sandpiper (*Actitis macularius*)	5	(Cialdini & Orians 1944) (*194*), (Miller & Miller 1948) (*195*), (Hays 1972) (*196*), (Oring & Knudson 1972) (*197*), (Alberico *et al*. 1991) (*198*)
82	Turnstone (*Arenaria interpres*)	2	(Kondratyev 1982) (*135*), (Perkins *et al.* 2007) (*199*)
83	Great Knot (*Calidris tenuirostris*)	1	(Tomkovich 2001) (*200*), P. Tomkovich unpublished data
84	Red Knot (*Calidris canutus*)	1	P. Tomkovich unpublished data
85	Sanderling (*Calidris alba*)	2	(Parmelee 1970) (*201*), (Hansen *et al.* 2010) (*202*), H. J. Hansen in litt.
86	Semipalmated Sandpiper (*Calidris pusilla*)	4	(Gratto *et al.* 1983) (*203*), (Moitoret *et al.* 1996) (*71*), (Sandercock 1997) (*204*), (Arctic Shorebird Demographics Network 2016) (*134*)
87	Western Sandpiper (*Calidris mauri*)	4	(Holmes 1972) (*205*), (Kondratyev 1982) (*135*), (Morozov & Tomkovich 1988) (*206*), (Sandercock 1997) (*204*)
88	Red-necked Stint (*Calidris ruficollis*)	1	(Morozov & Tomkovich 1988) (*206*)
89	Little Stint (*Calidris minuta*)	2	(Schekkerman *et al.* 2004) (*133*), (Arctic Shorebird Demographics Network 2016) (*134*)
90	Temminck's Stint (*Calidris temminckii*)	3	(Kondratyev 1982) (*135*), (Rönkä *et al*. 2003) (*207*), (Thompson *et al.* 2014) (*208*), P. Tomkovich unpublished data
91	Least Sandpiper (*Calidris minutilla*)	2	(Jehl 1971) (*139*), (Cooper and Miller 1997) (*140*)
92	White-rumped Sandpiper (*Calidris fuscicollis*)	2	(McKinnon & Bêty 2009) (*209*), (Arctic Shorebird Demographics Network 2016) (*134*)
93	Baird's Sandpiper (*Calidris bairdii*)	3	(Reid & Montgomerie 1985) (*210*), (McKinnon & Bêty 2009) (*209*), (Arctic Shorebird Demographics Network 2016) (*134*)
94	Pectoral Sandpiper (*Calidris melanotos*)	3	(Kondratyev 1982) (*135*), (Moitoret *et al.* 1996) (*71*), (Arctic Shorebird Demographics Network 2016) (*134*)
95	Sharp-tailed Sandpiper (*Calidris acuminata*)	1	(Soloviev *et al.* 2010) (*211*), (Arctic Shorebird Demographics Network 2016) (*134*), M. Soloviev in litt.
96	Curlew Sandpiper (*Calidris ferruginea*)	2	(Schekkerman *et al.* 1998) (*212*), (Schekkerman *et al.* 2004) (*133*)
97	Purple Sandpiper (*Calidris maritima*)	1	(Pierce *et al.* 2010) (*213*)
98	Rock Sandpiper (*Calidris ptilocnemis*)	1	P. Tomkovich unpublished data
99	Dunlin (*Calidris alpina*)	6	(Jehl 1971) (*139*), (Kondratyev 1982) (*135*), (Jönsson 1991) (*214*), (Moitoret *et al.* 1996) (*71*), (Jackson and Green 2000) (*99*), (Schekkerman *et al.* 2004) (*133*), (Arctic Shorebird Demographics Network 2016) (*134*)
100	Stilt Sandpiper (*Calidris himantopus*)	3	(Jehl 1971) (*139*), (Moitoret *et al.* 1996) (*71*), (Arctic Shorebird Demographics Network 2016) (*134*)
101	Spoon-billed Sandpiper (*Eurynorhynchus pygmeus*)	1	(Kondratyev 1982) (*135*)
102	Broad-billed Sandpiper (*Limicola falcinellus*)	1	(Soloviev *et al.* 2010) (*211*), (Arctic Shorebird Demographics Network 2016) (*134*), M. Soloviev & V. V. Golovnyuk in litt.
103	Buff-breasted Sandpiper (*Tryngites subruficollis*)	3	(Moitoret *et al.* 1996) (*71*), (Arctic Shorebird Demographics Network 2016) (*134*)
104	Ruff (*Philomachus pugnax*)	3	(Kondratyev 1982) (*135*), (Beintema & Müskens 1987) (*97*), (Arctic Shorebird Demographics Network 2016) (*134*)
105	Wilson's Phalarope (*Phalaropus tricolor*)	2	(Kagarise 1979) (*215*), (Kantrud & Higgins 1992) (*146*)
106	Red-necked Phalarope (*Phalaropus lobatus*)	5	(Moitoret *et al*. 1996) (*71*), (Walpole *et al.* 2008) (*216*), (Arctic Shorebird Demographics Network 2016) (*134*), M. Sládeček *et al*. in litt.
107	Red Phalarope (*Phalaropus fulicarius*)	2	(Moitoret *et al.* 1996) (*71*), (Arctic Shorebird Demographics Network 2016) (*134*)
108	Cream-coloured Courser (*Cursorius cursor*)	1	(Gonçalves 2014) (*217*), (Seymour *et al.* 2015) (*218*), Gonçalves in litt., K. Seymour in litt.
109	Double-banded Courser (*Rhinoptilus africanus*)	2	(Lloyd 2004) (*219*)
110	Collared Pratincole (*Glareola pratincola*)	1	(Hanane *et al.* 2010) (*220*)
111	Rock Pratincole (*Glareola nuchalis*)	2	(Brosset 1979) (*221*), (Williams *et al.* 1989) (*222*)

Species are taxonomically ordered according to IOC Word Bird List (ver. 6.3, 2016) (*35*). Complete references from this table are presented in the list of references.

Table S2. Nest predation in respect to time at different latitudes.

	Explantory variable	Daily nest predation				Total nest predation			
	Variable	Estimate	SE	*z-value*	*P-value*	Estimate	SE	*z-value*	*P-value*
A, All data	(Intercept)	-31.6090	5.014			-11.5451	2.115		
n = 237 populations	Mean year	0.0142	0.003	5.63	< 0.001	0.0060	0.001	5.68	< 0.001
	log(Number of nests)	-0.0125	0.031	-0.4	0.690	-0.0005	0.013	-0.04	0.970
B, Subset of data – South temperate	(Intercept)	-21.5452	16.998			-6.1223	7.278		
latitudes from -62° to -30°	Mean year	0.0087	0.009	1.02	0.310	0.0031	0.004	0.86	0.390
n = 24 populations	log(Number of nests)	0.1022	0.119	0.86	0.390	0.0527	0.050	1.48	0.300
C, Subset of data – South tropics	(Intercept)	-11.2810	24.045			-4.7111	10.269		
latitudes from -30° to 0°	Mean year	0.0036	0.012	0.30	0.770	0.0025	0.005	0.47	0.630
n = 14 populations	log(Number of nests)	0.1494	0.135	1.11	0.270	0.0627	0.057	1.09	0.280
D, Subset of data – North tropics	(Intercept)	-10.5856	16.083			-1.3468	7.375		
latitudes from 0° to 30°	Mean year	0.0040	0.008	0.49	0.620	0.0010	0.004	0.29	0.770
n = 17 populations	log(Number of nests)	-0.1220	0.086	-1.42	0.150	-0.0475	0.039	-1.21	0.230
E, Subset of data – North temperate	(Intercept)	-33.1301	7.52			-13.9012	3.163		
latitudes from 30° to 60°	Mean year	0.0150	0.004	3.98	< 0.001	0.0072	0.002	4.58	< 0.001
n = 96 populations	log(Number of nests)	-0.041	0.043	-0.95	0.340	-0.0204	0.018	-1.14	0.250
F, Subset of data – Arctic	(Intercept)	-40.1497	8.215			-14.281	3.396		
latitudes from 60° to 78°	Mean year	0.0186	0.004	4.48	< 0.001	0.0075	0.002	4.35	< 0.001
n = 86 populations	log(Number of nests)	-0.0409	0.064	-0.63	0.530	-0.0164	0.027	-0.62	0.54

Linear mixed-effects kinship models with control for phylogeny (species level of phylogeny + random effect of the species), spatial autocorrelation and number of nests per population, see (*19*) for details. Mean year = the mean year of the data collection, log(N number of nests) = logarithm of the number of nests.

Table S3. Robustness of temporal trend in nest predation to shorebird clades and daily nest predation computation method.

	Explanatory variable	Daily nest predation				Total nest predation			
	Variable	Estimate	SE	*z-value*	*P-value*	Estimate	SE	*z-value*	*P-value*
A, All data	(Intercept)	-31.6090	5.014			-11.5451	2.115		
n = 237 populations	Mean year	0.0142	0.003	5.63	< 0.001	0.0060	0.001	5.68	< 0.001
	log(Number of nests)	-0.0125	0.031	-0.4	0.690	-0.0005	0.013	-0.04	0.970
B, Subset of data – Charadrii	(Intercept)	-27.007	8.574			-9.7587	3.660		
n = 110 populations	Mean year	0.0118	0.004	2.74	0.006	0.0051	0.002	2.79	0.005
	log(Number of nests)	0.0063	0.046	0.14	0.890	0.0025	0.020	0.13	0.900
C, Subset of data – Scolopaci	(Intercept)	-37.7680	6.181			-13.4618	2.630		
n = 127 populations	Mean year	0.0173	0.003	5.58	< 0.001	0.0070	0.001	5.32	< 0.001
	log(Number of nests)	-0.0069	0.044	-0.16	0.870	-0.0028	0.018	-0.15	0.880
D, Subset of data – given DPR	(Intercept)	-27.8193	9.192			-9.1600	3.734		
n = 97 populations	Mean year	0.0125	0.005	2.73	0.006	0.0049	0.002	2.65	0.008
	log(Number of nests)	-0.0863	0.047	-1.82	0.068	-0.0283	0.019	-1.48	0.140
E, Subset of data – computed DPR	(Intercept)	-25.6157	6.262			-10.0549	2.754		
n = 140 populations	Mean year	0.0110	0.003	3.47	< 0.001	0.0052	0.001	3.74	< 0.001
	log(Number of nests)	0.0719	0.042	1.72	0.085	0.0347	0.018	1.89	0.059

Linear mixed-effects kinship models with control for phylogeny (species level of phylogeny + random effect of the species), spatial autocorrelation and number of nests per population, see (*19*) for details. Mean year = the mean year of the data collection, log(N number of nests) = logarithm of the number of nests.

Table S4. Within-population variation in historic and recent nest predation.

Species	Location	Latitude	Longitude	Period	DPR	SE	TPR (%)	Years	Mean year	N nests	Exposure
Northern Lapwing	Czech Rep.	49.115	14.268	historic	0.023	0.002	50.64	10	1993	375	6883
Vanellus vanellus				recent	0.044	0.002	65.84	8	2006	505	6694.8
Hudsonian Godwit	Canada	58.701	-93.802	historic	0.005	0.005	13.53	4	1965	12	186.3
Limosa haemastica				recent	0.034	0.012	60.67	3	2013	21	235.5
Whimbrel	Canada	58.701	-93.802	historic	0.018	0.004	40.78	6	1969	80	1172.8
Numenius phaeopus				recent	0.050	0.006	77.37	4	2012	138	1481.5
Common Greenshank	Scotland	58.533	-4.232	historic	0.018	0.011	40.40	18	1992	24	275.925
Tringa nebularia				recent	0.027	0.011	53.81	7	2004	27	297.15
Sanderling	Greenland	74.478	-20.555	historic	0.019	0.008	44.53	4	1997	36	365.8
Calidris alba				recent	0.054	0.010	74.95	6	2003	38	405.7
Western Sandpiper	Alaska	64.449	-164.977	historic	0.027	NA	49.20	3	1994	126	1071
Calidris mauri				recent	0.050	0.005	72.26	3	2013	196	2280
Temminck's Stint	Finland	65.021	24.72	historic	0.026	0.003	47.60	19	1992	424	4642.56
Calidris temminckii				recent	0.039	0.007	62.45	4	2004	76	877.92
Pectoral Sandpiper	Alaska	70.380	-149.534	historic	0.011	0.003	25.67	4	1990	123	1762.8
Calidris melanotos				recent	0.051	0.017	74.56	2	2011	18	195
Dunlin	Canada	58.701	-93.802	historic	0.000	NA	0.00	4	1965	13	195
Calidris alpina				recent	0.017	0.004	34.62	4	2012	114	1483.5

Historic values are prior 2000 and recent after the year 2000, DPR = daily nest predation, TPR % = total nest predation values, Years refer to the number of breeding seasons involved, exposure is given in days. Standard error computation follows Johnson (*65*); it was impossible to compute it in the historic period for Western Sandpiper because the number of all failed nests was not given and for the Dunlin due to zero nest predation. For data sources see table S1. Species are taxonomically ordered according to IOC Word Bird List (ver. 6.3, 2016) (*35*).

Table S5. Within-population variation in historic and recent nest predation – statistics.

Explanatory variable	**Daily nest predation**				**Total nest predation**			
Variable	Estimate	SE	*t-value*	*P-value*	Estimate	SE	*t-value*	*P-value*
(Intercept)	-3.8687	1.033			0.3572	0.457		
Period	0.5475	0.216	2.54	< 0.001	0.2698	0.092	2.93	< 0.001
Latitude	0.0115	0.016	0.71	0.414	0.0042	0.007	0.58	0.508

Linear mixed effect model with the random effect of species, n = 9 populations, for details see table S4.

Table S6. Effect of latitude (A, B and C) and time (A) on nest predation.

	Explanatory variable	Daily nest predation				Total nest predation			
	Variable	Estimate	SE	*z-value*	*P-value*	Estimate	SE	*z-value*	*P-value*
A, All data	(Intercept)	-33.6843	4.841			12.3737	2.058		
n = 237 populations	Mean year	0.0151	0.004	6.21	< 0.001	0.0064	0.001	6.20	< 0.001
	Hemisphere	0.4205	0.109	3.86	< 0.001	0.1653	0.046	3.57	< 0.001
	abs(Latitude)	-0.0011	0.002	-0.45	0.650	-0.0008	0.001	-0.73	0.470
	log(Number of nests)	-0.0158	0.031	-0.52	0.520	-0.0016	0.013	-0.12	0.910
separate model for interaction effect	Mean year : Hemisphere	0.0047	0.008	0.58	0.560	0.0027	0.003	0.82	0.410
separate model for interaction effect	Mean year : abs(Latitude)	0.0002	< 0.001	1.72	0.086	0.0001	< 0.001	1.51	0.130
separate model for interaction effect	Hemisphere : abs(Latitude)	0.0143	0.008	1.71	0.087	0.0058	0.004	1.65	0.099
B, Subset of historic data	(Intercept)	-3.174	0.477			0.6473	0.239		
(before year 2000)	Hemisphere	0.2864	0.23	1.25	0.210	0.1001	0.102	0.98	0.330
n = 145 populations	abs(Latitude)	-0.0158	0.005	-3.42	< 0.001	-0.0079	0.002	-3.75	< 0.001
	log(Number of nests)	0.0093	0.039	0.24	0.810	0.0010	0.017	0.06	0.950
separate model for interaction effect	Hemisphere : abs(Latitude)	0.0083	0.013	0.62	0.530	0.0035	0.006	0.58	0.560
C, Subset of recent data	(Intercept)	-3.8556	0.312			0.2973	0.128		
(after year 2000)	Hemisphere	0.3141	0.172	1.82	0.068	0.1260	0.073	1.73	0.084
n = 102 populations	abs(Latitude)	0.0063	0.004	1.74	0.081	0.0020	0.001	1.34	0.180
	log(Number of nests)	0.0173	0.051	0.34	0.730	0.0140	0.021	0.65	0.510
separate model for interaction effect	Hemisphere : abs(Latitude)	0.0296	0.013	2.18	0.029	0.0137	0.006	2.42	0.015

Linear mixed-effects kinship models with control for phylogeny (species level of phylogeny + random effect of the species), spatial autocorrelation and number of nests per population. The sum of historic and recent nest predation values is 247 data points because 10 populations were divided into two subsets, see (*19*) for details. Mean year = the mean year of the data collection, Hemisphere = Northern and Southern hemisphere, abs(Latitude) = absolute value of latitude, log(N number of nests) = logarithm of the number of nests.

Table S7. Climate change in relation to nest predation.

Explanatory variable	Daily nest predation				Total nest predation			
Variable	Estimate	SE	*z-value*	*P-value*	Estimate	SE	*z-value*	*P-value*
(Intercept)	-3.5592	0.157			0.3913	0.070		
Temperature slope 30	6.7453	1.283	5.26	< 0.001	2.6798	0.545	4.92	< 0.001
log(Number of nests)	-0.0030	0.031	-0.10	0.920	0.0026	0.013	0.20	0.840
(Intercept)	-3.6164	0.158			0.3694	0.071		
Temperature slope 40	8.2550	1.624	5.08	< 0.001	3.2853	0.690	4.76	< 0.001
log(Number of nests)	0.0108	0.031	0.34	0.730	0.0077	0.013	0.57	0.570
(Intercept)	-3.5224	0.165			0.4064	0.072		
Temperature slope 20	4.2774	0.986	4.34	< 0.001	1.6618	0.418	3.98	< 0.001
log(Number of nests)	-0.0012	0.032	-0.04	0.970	0.0036	0.014	0.27	0.790
(Intercept)	-3.4399	0.167			0.4376	0.073		
Temperature slope 10	0.4612	0.415	1.11	0.270	0.1571	0.175	0.90	0.37
log(Number of nests)	0.0017	0.033	0.05	0.960	0.0051	0.014	0.37	0.72
(Intercept)	-3.7941	0.198			0.3206	0.0872		
Temperature sd 30	0.3852	0.132	2.91	0.004	0.1268	0.057	2.23	0.026
log(Number of nests)	0.0245	0.033	0.74	0.46	0.0127	0.014	0.90	0.370
(Intercept)	-3.8524	0.198			0.2982	0.088		
Temperature sd 40	0.4315	0.129	3.34	0.001	0.1456	0.055	2.63	0.009
log(Number of nests)	0.0277	0.033	0.84	0.400	0.0138	0.014	0.99	0.32
(Intercept)	-3.7188	0.198			0.3508	0.087		
Temperature sd 20	0.3049	0.129	2.36	0.018	0.0944	0.055	1.71	0.087
log(Number of nests)	0.0217	0.033	0.65	0.510	0.0115	0.014	0.81	0.420
(Intercept)	-3.5757	0.185			0.3951	0.081		
Temperature sd 10	0.1852	0.123	1.50	0.130	0.0576	0.052	1.10	0.270
log(Number of nests)	0.0110	0.033	0.33	0.740	0.0081	0.014	0.58	0.560

N = 247 population measurements (10 populations were divided into two subsets), see (*19*) for details and climatic variables preparation.

Table S8. Correlation matrix of four potential predictors of nest predation.

Correlation matrix (Spearman's rank correlation)				
Variable	Latitude	Year	Temperature slope 30	Temperature sd 30
Latitude	1			
Mean year	-0.003	1		
Temperature slope 30	0.230	0.672	1	
Temperature sd 30	0.701	0.202	0.484	1
Correlation matrix with Spearman's correlation test P-values				
Variable	Latitude	Year	Temperature slope 30	Temperature sd 30
Latitude				
Mean year	0.115			
Temperature slope 30	< 0.000	< 0.001		
Temperature sd 30	< 0.001	0.001	< 0.001	

N = 247 population measurements (10 populations were divided into two subsets), see (*19*) for details.

Grey-tailed Tatler (*Tringa brevipes*) stretching in its preffered habitat, Golden Ridge, Chukotka, Russia, 2015

Chapter 12

Linking population trends with species' traits and threats: a global analysis of shorebirds as a case study

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(under the review)

Linking population trends with species' traits and threats: a global analysis of shorebirds as a case study

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Linking population trends to species' traits is informative for detection of most important threats and for assessing conservation effectiveness. Here we used information on global population trends of shorebirds, a widely distributed and ecologically diversified bird group, and related their population declines and increases to species' traits, threats and conservation concerns. We found population declines in the majority of species and these were more likely in species with shorter generation times and longer migration distances. Declining species were threatened by habitat deterioration, climate change and direct human persucution. These results indicate that short generation time is probably disadvantageous in the recent era of global environmental change because such species cannot postpone their reproduction and are forced to reproduce in suboptimal conditions. Decline in long-distance migrants was related to climate change which is particularly rapid in the Arctic where these migrants most often breed. On the hand, migrants' declines were not associated with any specific flyway or migration strategy indicating their likely global occurrence. A positive message may be that a higher number of scientific studies focused on declining species than on the others suggesting that the evidence-based conservation likely matters in shorebirds. We also found that the global population increases are associated with island endemics suggesting a success of conservation actions in these species, although they are threatened by introduced predators. However, these examples are still quite rare and wider conservation effort is needed to improve the population status of shorebirds, especially those with short generation times and long-distance migrants.

Keywords: waders, population dynamics, migration strategy, life history strategy, island endemism, climate change, habitat deterioration, conservation

Introduction

Global biodiversity faces a serious extinction crisis (Pimm *et al.*, 2014) and population trends are among the most important indicators showing temporal trajectory in the state of nature (Butchart *et al.*, 2010). Moreover, population trends serve as a key measure for the assessment of extinction risk within the IUCN Red List criteria (Mace *et al.*, 2008) and other frameworks (Boyd *et al.*, 2017). At the same time, population trends are highly informative for conservation practitioners, providing biologically relevant data about the success or failure of conservation actions (Greenwood, 2003). It contrasts to the economic measures such as the amount of funding sources consumed or the number of people employed for a given conservation action (Ferraro & Pattanyak, 2006).

In birds, various traits were hypothesized to be related to population declines and increases (see Reif, 2013 for review). Nevertheless, we are not aware of any studies providing results at a global scale encompassing the trends for entire populations of the species of interest. Such global analyses are the most relevant for species conservation in terms of overall population deterioration (potentially leading to irreversible loss of a given species) and improvement (signifying global success). Here we aim to fill this knowledge gap in conservation science by performing a global-scale analysis of the traits linked to population trends and potential threats for shorebirds, a highly diverse and globally distributed bird group. They occupy most biomes and biogeographic zones and show high diversity in breeding habitats, generation time, migratory behaviour and geographic range sizes (Hayman, Marchant & Prater, 1986; del Hoyo, Elliott & Sargatal, 1996; Colwell, 2010). Moreover, several studies reported severe declines of shorebirds in some regions (e.g. Galbraith *et al.*, 2014; Thomas, Lanctot & Szekely, 2006) and a global analysis of their trends to test possible drivers is urgently needed (Munro, 2017).

We specifically focused on the following traits of shorebird species for which the hypothesized relationships to population trends and threats were described in the literature. (i) Species' habitat association is considered to be a key trait directly showing population consequences of changes in habitat area and quality (Schmidt, 2017). Species using a given habitat decline if this habitat deteriorates and vice versa (Ducatez & Shine, 2017). (ii) Together with habitat change, climate change is an increasingly important driver of bird population changes (Scheffers *et al.*, 2016), as reflected by the trends of species with different climatic niches: warm-adapted species generally increase, whereas cold-adapted birds decline (Stephens *et al.*, 2016). (iii) Under conditions of these recent global environmental changes, species life history strategy may play an important role (Jiguet *et al.*, 2007). In the case of shorebirds with their nearly invariant clutch size and breeding often limited to a single attempt per year, generation time seems to be a crucial factor shaping productivity of populations (Colwell, 2010; del Hoyo *et al.*, 2016). It can be hypothesized that the species with longer generation time and longer life span have more opportunities to reproduce during their life (Sol, *et al.* 2012). They should be thus more resilient to impacts of global changes indicated by their less negative population trends compared to the species with shorter generation time. However, generation time is positively correlated with body size and larger species may be more sensitive to human disturbance and more attractive to hunters (Owens & Bennett, 2000). We can thus predict that species with longer generation time will be more exposed to these

threats. (iv) Small populations are more prone to the effects of demographic and environmental stochasticity and thus at a higher risk of extinction (Sæther *et al.*, 2005). Since population size and geographic range size closely covary (Rahbek & Borregaard, 2010), geographic range size is often considered as a trait linked to bird population trends (Reif, 2013) and within the small-ranged species, island endemics are considered as particularly vulnerable (Purvis *et al.*, 2000). This vulnerability of island endemics is caused by their higher sensitivity to introduced predators and novel parasites in addition to threats caused by small population size *per se* (Whittaker *et al.*, 2017). (v) Finally, species vary in the intensity they are studied, as well as in the effort devoted to their conservation. It has been shown that these factors are related to species' extinction risk when more resources are invested into more threatened species (Brooke *et al.*, 2008) but such species are less intensively studied at the same time (Ducatez & Shine, 2017). Although relationships of these measures to population trends remain to be explored, we predict that higher effort from the side of researchers and conservationists should be targeted on more declining species.

There are indications that migratory shorebirds may be at particular risk of population decline (Munro, 2017; Studds *et al.*, 2017) and thus we paid special attention to these species, focusing on their following traits. (i) Migration is costly in terms of energy demands and refuelling at stop-over sites exposes birds to predators (Alves *et al.*, 2013). Therefore, migration distance (i.e. distance between species breeding and non-breeding area) should be negatively correlated with species' population trend. (ii) Species vary in migration strategies in terms of following the coastal vs. inland habitats (Piersma, 2003). There are several indications that coastal areas suffer from greater habitat change due to their attractiveness to human economic and free-time activities (Studds *et al.*, 2017). (iii) Location of a given migration route may be decisive for the fate of migrating individuals because some areas suffer from habitat deterioration or human disturbance more than the others (Thomas *et al.*, 2006; Hewson *et al.*, 2016). (iv) Negative influence of threats during migration can be buffered by high migratory dispersion of individuals in non-breeding relative to breeding ranges as recently suggested by Cresswell (2014). Species with relatively larger non-breeding than breeding ranges should enjoy greater buffering effect resulting in less negative trends of species with higher migratory dispersion (Gilroy *et al.*, 2016).

In this study, we test the predictions formulated above within a framework encompassing three sets for analyses enabling deep understanding of the whole system. First, we relate population trends to species' traits to identify intrinsic factors contributing to the global population changes. Second, we relate population trends to threats and conservation concerns to determine external drivers making the species at risk. Third, we relate species' traits to particular threats and conservation concerns to learn what are the species' characteristics making them sensitive to environmental change. By that means our analyses provide a complex overview of the pathways leading from potential drivers to population responses.

Materials and Methods

Species selection and population trends

As "shorebirds" we consider species classified into the order Charadriiformes according to the traditional definition, i.e. excluding gulls, terns and auks, which is reasonable from the perspective of eco-morphological coherence of the focal species. From 245 extant shorebird species, 197 species have known population trends released by BirdLife International (2016). To reconcile the dataset with the phylogenetic information in Jetz *et al.* (2012), which was used for the analyses and did not reflect some recent taxonomic modifications that appeared in the BirdLife International (2016), we merged such recently separated taxa back together with the parental species to obtain the final dataset of 184 species (Supplementary Table 1). Therefore, our final dataset contains 75% of all shorebird species currently living on Earth.

For each species, we extracted information on its population trend between 2001 and 2012 from BirdLife International (2016). BirdLife International (2016) recognized three trend categories: population increase, decline and stability (Supplementary Table 1). These trend categories were reflected by two separate analyses – one for population declines and one for population increases. Following the approach applied in a recent study of Gilroy *et al.* (2016), we coded declines as 1 and remaining trend categories as 0 to focus on the relationships between traits and population declines. Similarly, we coded increases as 1 and remaining trend categories as 0 to focus on the relationships between traits and population increases.

Species' traits

From various literature sources specified below, we collected literature data on life history strategy, habitat, migration distance, absolute breeding latitude and island endemism for all 184 species. In addition, we collected data on migratory dispersion, migratory flyway and migration strategy for 95 species of migrants.

To express species' life history strategy, we used data on their *generation time* (in years) provided by BirdLife International (2016). We also extracted data on mean body mass of each species from the Handbook of the Birds of the World Alive (del Hoyo *et al.*, 2016). However, it was closely positively correlated with generation time ($r = 0.7$, after log-transformation), so we decided to keep the former variable in our dataset due to its more straightforward link to life histories, which is not the case for body mass (Blackburn, Lawton & Gregory, 1996).

For each species, we collected information on their habitat from del Hoyo *et al.* (2016). Based on this information, we discriminated two breeding habitat gradients and recognized position of each species along each gradient: *habitat openness* (1 - forest, woodland or dense scrubland; 2 - sparse woody vegetation; 3 - grassland, open habitats with low vegetation cover) and *habitat aridity* (1 - humid habitats; 2 - mesic habitats; 3 - arid habitats). Moreover, we recorded whether (1) or not (0) a given species occurs in *artificial habitats* (e.g. cropland, rice fields, saltpans).

For migration distance, absolute breeding latitude and island endemism were estimated using shape-file data underlying species' geographic range maps in BirdLife International and NatureServe (2014). In QGIS 2.16.3 (QGIS Development Team, 2016), we calculated geographic coordinates of centroids of species' breeding and non-breeding ranges.

Following Albrecht *et al.* (2013), we considered the distance between these centroids as *migration distance* in km. *Absolute breeding latitude* was calculated as a distance (in degrees) of the centroid of the breeding range of given species from the equator. As *island endemics* we considered species whose both breeding and non-breeding ranges were confined to islands and did not overlap any of the continents.

As migratory, we considered the species with migration distance longer than 500 km. Although this division line is arbitrary, it effectively discriminates the species having largely overlapping breeding and non-breeding ranges or those undergoing only erratic seasonal movements from true migrants. For migrants, we calculated *migratory dispersion* based on areas of species' breeding and non-breeding ranges applying the formula from Gilroy *et al.* (2016) obtaining dimensionless values from -1 to 1. It expresses dispersion as the area of non-breeding range relative to the area of breeding range. Concerning migratory flyways, we used information of eight major flyways (*Pacific Americas*, *Mississippi Americas*, *Atlantic Americas*, *East Atlantic*, *Black Sea / Mediterranean*, *West Asia / East Africa*, *Central Asia*, *East Asia / Australasia*) from Boere & Stroud (2006) and Delany *et al.* (2009) assigning each species to one or more of them (1 - a species uses a given flyway, 0 - a species does not use a given flyway). For *migration strategy*, we discriminated species migrating or wintering along the coast (categorized as 1) from species with inland migration and wintering (0) and species showing both strategies (0.5).

Species' threats and conservation concerns

Based on the information in BirdLife International (2016), we recorded presence (1) and absence (0) of following four major threats factors for each species: *habitat deterioration* (any type of human-induced alteration in habitat quantity or quality), *climate change* (any type of climate change consequences including severe weather), *direct human persecution* (hunting and other types of utilisation, intrusion and disturbance) and *biotic interactions* (threats from invasive or native problematic species or diseases).

We also collected data on two variables expressing scientists' and conservationists' interest towards each species – the *number of scientific studies* focused on a given species and the *proportion of these studies that are focused on species' conservation*. For this purpose, we run a search on Web of Science using species scientific name (considering also recent taxonomic changes such as *Calidris pugnax* and *Philomachus pugnax* for Ruff) in November and December 2016. The number of studies revealed by this search was considered as a measure of the interest in this species from the scientists' point of view. In the next step, we scanned the abstracts of these studies to discriminate those focused on conservation from the remaining ones. We classified as studies focused on species' conservation those describing management options for a given species, assessing conservation measures applied or classifying species' population status in relation to conservation measures. The studies focused on species' ecology with conservation implications, as well as studies describing human pressures upon a given species without any notes on conservation actions, were not included among the studies expressing conservationists' interest. The proportion of studies focused on species' conservation from the total number of all scientific studies focused on a given species was taken as a measure of conservationists' interest.

Statistical analysis

Before performing any analyses, we performed pairwise correlations for explanatory variables to identify any potential issues with collinearity (Supplementary Table 2). These correlations were calculated separately for each group of variables corresponding to particular sets of statistical models described below, i.e. (i) trait variables of all species, (ii) threats and consevation concerns of all species and (iii) trait variables of migrants (Supplementary Table 2). We found that migration distance and absolute breeding latitude were highly correlated ($r = 0.82$) and we thus excluded the latter variable from the analyses of all species traits. Moreover Black Sea / Mediterranean flyway was highly correlated with both East Atlantic flyway ($r = 0.77$) and West Asia / East Africa flyway ($r = 0.87$). Black Sea / Mediterranean flyway was thus excluded from the analyses of migratory species.

We first focused on the dataset with the traits of all species ($n = 184$) performing three sets of analyses: (i) analyses relating population trends (response variable) to the species' traits (fixed-effects explanatory variables); (ii) analyses relating population trends (response variable) to the threats and the measures of scientific and conservation interest (fixed-effects explanatory variables); (iii) analyses relating the threats and the measures of scientific and conservation interest (response variable) to species' traits (fixed-effects explanatory variables). In the analyses of species population trends (i.e. the analyses (i) and (ii), respectively), we always run a separate set of models having population decline, and population increase as respective response variables. In the last set of analyses (iii), we run separate sets of models for each species' threat and a measure of conservation concern used as a distinct response variable.

The kind of the models applied in respective analyses was dictated by the nature of the response variable. Both population trends and threats were binomial variables with values of 1 or 0. Therefore, all models used in the analyses (i) and (ii) and a first part of the models used in the analyses (iii) were generalized mixed-effects models (GLMMs) with binomial error distribution and logit link function. For the analyses with the measures of scientific and conservation interest (the second part of the models in the analyses (iii)), we used GLMMs with normal error distribution and identity link function. The random effects part of all models in all sets of analyses contained taxonomic level family as a random intercept to account for possibly similar trends of more closely related species (see Gamero et al. 2017).

In all analyses, we applied information-theoretic approach based on Akaike Information Criterion corrected for small sample sizes (AIC_c) to infer statistical effects of the focal variables. For each response variable, we composed a set of models containing all possible combinations of explanatory variables. We defined the main-effects models only because we did not have any predictions for interactions among the focal explanatory variables. For each model in a given set, we expressed its performance using AIC_c and caculated accompanying measures (i.e. ΔAIC_c, number of model parameters and model weight). Then we ordered the models according to increasing AIC_c and made inference. For the inference, we used a subset of the models with $\Delta AIC_c < 2$ (Burnham & Anderson 2002) and expressed the statistical effects of particular explanatory variables by averaging of their estimates using weights of the models containing respective variables (Johnson & Omland

2004). After obtaining these model-averaged parameter estimates, we considered a given variable as important if its 95% confidence interval (CI) did not overlap zero.

In the next step, we focused on the relationships between population declines and specific traits of migratory species (n = 95). Population trend was the response variable and particular traits of migrants were the fixed-effects explanatory variables. We run GLMMs with binomial error distribution and logit link function in the same way as in the dataset containing all species.

All models were run in R version 2.12.0 (R Development Core Team, 2010) using the packages 'lme4' (Bates et al. 2015) for generalized mixed-effects modelling and 'MuMIn' (Bartoń 2009) for multimodel inference based on information-theoretic approach.

Generation time was log-transformed and all explanatory variables were standardized to zero mean and unit variance before analysis to make their statistical effects directly comparable.

Results

Population trends of waders can be generally characterized as decreasing: from 184 species included in our analysis, 105 declined and only 19 increased, whereas remaining 60 species had stable populations (Supplementary Table 1). Within the subset of 95 migratory species, population declines were even more predominant as they were observed in 64 species, while only five species increased and 26 species were stable (Supplementary Table 1).

Population declines

When considering all species together, all models within the subset of the best performing models ($\Delta AIC_c < 2$) contained variables generation time and migration distance (Table 1a). Each of the variables habitat openness and habitat arid appeared in one of these best performing models (Table 1a) but their model-avereged CIs overlapped zero (Table 1b) indicated their limited ability to explain shorebird population declines. In contrast, generation time and migration distance were important predictor of shorebird decline as their CIs did not overlap zero (Table 1b). Statistical effects of these variables (Table 1b) showed that the species more likely to undergo population declines were those with a shorter generation time and migrating over longer distances (Fig. 1).

In the analyses of threats and conservation concerns, we found that shorebird declines were mostly related to habitat deterioration, climate change and direct human persecution, and that declining species were more often subjects to scientific studies (Table 2). All these variables were included in all models within the subset of the best performing models (Table 2a) and their CIs did not overlap zero (Table 2b). One of the best performing models contained also biotic interactions and another one proportion of studies focused on species' conservation, but CIs of these two variables overlapped zero (Table 2b).

Focusing on population declines of migrants, our information-theoretic approach did not find support for any of the variables considered. Indeed, the best performing model did not contain any predictors but intercept only (Table 3a). Although several explanatory

variables such as migration strategy and some specific flyways were included in the remaining models within the subset of the models with $\Delta AIC_c < 2$ (Table 3a), CIs of all these variables overlapped zero (Table 3b). Therefore, our analysis showed that population declines of migratory shorebirs are not linked to any specific flyway or to species migrating specifically through coast or inland.

Population increases

For all species together, we indentified nine models as those with $\Delta AIC_c < 2$ (Table 4a). All these models contained the variable island endemism (Table 4a) and it was the only variable with CI not overlapping zero (Table 4b) indicating important statistical effect on shorebird population increase. Specifically, the species more likely to undergo population increase were the island endemics (Table 4b). Although only 8.7% of the focal shorebird species were island endemics, they account for 31.6% of population increases in our dataset. Generation time occurred in seven of the best performing models (Table 4a) but its CI marginally overlapped zero indicating that species with longer generation time were more likely to increase but support for this relationship was not strong enough (Table 4b). Several models of the best performing subset contained habitat variables (namely openness, aridity and artificial habitats) and migration distance but their CIs largely overlapped zero (Table 4b).

When focusing on threats and conservation concerns, we found that shorebird population increases were related only to biotic interactions which the variable included in all seven best performing models (Table 5a) and its CI did not overlap zero (Table 5b). It showed that species threatened by this factor were more likely to increase (Table 5b). Although climate change, habitat loss and direct human persecution were included in five to six of the best performing models (Table 5a), their CIs always overlapped zero (Table 5b) indicating that these variables were unrelated to shorebird population increases.

Relating traits to species' threats and conservation concerns

Our information-theoretic approach found that habitat loss (Supplementary Table 3) and proportion of studies focused on species' conservation (the only model with $\Delta AIC_c < 2$ was the one containing solely the intercept; AIC_c weight = 0.517) were unrelated to any of the species' traits. In the case of climate change, we all four best performing models contained the variable migration distance (Supplementary Table 4a) and it was also the only variable whose CI did not overlapp zero (Supplementary Table 4b). The model-averaged coefficient indicated that the species migrating on longer distance were more likely threatened by climate change (Supplementary Table 4b). In the case of direct human persecution, all five best performing models contained the variable generation time (Supplementary Table 5a) and it was the only variable with CI not overlapping zero (Supplementary Table 5b). Species with longer generation time were more likely to be persecuted by humans (Supplementary Table 5b). Models analysing relationships of species' traits to biotic interacions showed that two variables, artificial habitat and island endemism, were included within the best performing models (Supplementary Table 6a) and their CIs did not overlap zero at the same time (Supplementary Table 6b). According to the model-averaged coefficients, island endemics were more likely to be threated from biotic interactions, whereas opposite was observed in the species occrring in artifucial habitats (Supplementary Table 6b). Finally, number of scientific

studies was related to migration distance and generation time (Supplementary Table 7a), when species migrating with longer generation time and migrating on longer distances were more intensively studies (Supplementary Table 7b).

Discussion

Our analysis of a global dataset on population trends of 184 species of shorebirds (representing 75% of all extant members of this group) found that more than half of these species declined, indicating unfavourable conservation status of this bird group as a whole. Population declines were strongly related to migration distance and we found that global populations in more than two thirds of migrants were declining. Considering the other ecological traits, shorebird declines were linked with short generation time, but not with species' habitat associations. However, habitat deterioration was an important driver of shorebird population decline together with climate change and direct persecution by humans, whereas biotic interactions were unrelated to declines. In addition, declining species and species migrating on longer distances were more often subject of scientific studies. By contrast, species endemic to islands showed population increases, but were more often threatened by biotic interactions.

These results indicate that species' life history and migration strategy together with geographic range size characteristics are more important traits than species' habitat associations for coping with recent environmental challenges. In the light of the recent studies showing a clear habitat clustering of variability in bird population trends (e.g. Jorgensen *et al.*, 2016; Schipper *et al.*, 2016), such as declines of species preferring open habitats due to agricultural intensification (Butler *et al.*, 2010), this finding is somewhat surprising. Since we identified habitat deterioration as one of the important threats related to shorebird declines, there is a strong indication that such deterioration is not associated with some specific habitats but acts across different habitat categories. However, we should be cautious in generalizing this finding to other groups of organisms that may largely differ from shorebirds in their habitat use.

Life history strategy is one of the traits that associated with population response to recent global changes (Jiguet *et al.*, 2007). In the case of our data, the relationships confirmed our expectation that species with longer generations will decline less than species with shorter generations. The mechanistic explanation is provided by Sol *et al.* (2012). They suggest that if the suitability of environmental conditions varies over time and only rarely approaches optimum values, as is the case with recent human-induced environmental perturbations, then only the species being able to wait for longer time for reproduction, i.e. species with longer generations having longer life span, could exploit the favourable conditions and successfully reproduce. Although longer generation time makes species somewhat more prone to direct persecution by humans as we found here, this threat is insufficient to make species with longer generations at risk globally. In contrast, species with high population turnover will reproduce more frequently in suboptimal conditions potentially leading to their decline. This is also supported by nearly significant association with the threat from habitat deterioration

for short-generation species and the general importance of habitat deterioration as a driver of shorebird decline.

Migration over longer distances seems to be risky for shorebird species as it is significantly associated with declines at the global scale which corresponds to findings of recent continent-level (Galbraith *et al.*, 2014), as well as local-level studies (Simmons *et al.*, 2015). This pattern might be explained by the fact that migration *per se* is highly energy demanding and the need for refuelling exposes migratory birds to predators that may cause the population decline (Studds *et al.*, 2017). However, we did not find that biotic interactions (including predation) would threaten migratory shorebird species. Instead, we found that increasing shorebirds' migration distance is positively associated with the threat from climate change. What could be the mechanism underlying this pattern? In general, long-distance migrants are less flexible in adjustment of their breeding phenology to spring advancement caused by climate change than short-distance migrants or residents (Gill *et al.*, 2014). Phenological mismatch between different trophic levels is stronger for species migrating for longer distance and they can thus suffer from reduction of food supply (Both *et al.*, 2010; van Gils *et al.*, 2016). Moreover, more intensive interspecific competition with residents or short-distance migrants can also make long-distance migrants more severely affected by the climate change (Ahola *et al.*, 2007).

However, besides these general mechanisms, we suggest an additional shorebird-specific driver linking population declines of migrants to climate change. Since the longest-distance migrants are the species breeding at high latitudes at the same time (see Supplementary Table 2), we suggest that these species suffer from quickly progressing climate change in the Arctic (Holland & Bitz, 2003). Shorebirds are well-known as alternative prey to lemmings for Arctic predators (Meltofte *et al.*, 2007; McKinnon, Berteaux, & Bêty, 2014). Therefore, the collapse of lemming populations at many Arctic locations (Aharon-Rotman *et al.*, 2014) due to a higher frequency of rain-on-snow conditions during winter time (Kausrud *et al.*, 2008) may result in increased predation pressure on shorebirds' nests and chicks (Meltofte *et al.*, 2007). Indeed, the links between deteriorating shorebirds' breeding performance and population decline were already described locally (Descamps *et al.*, 2017; Munro 2017; Wauchope *et al.*, 2017) and here we highlight their possible signature on global trends.

Another source of threat for migrating species is the situation at stop-over sites and in wintering quarters (Thomas *et al.*, 2006) where the human pressure accelerated over the past few decades (Vickery *et al.*, 2014). Several recent studies found that species migrating or wintering along the East Asian / Australasian flyway decline (e.g. Piersma *et al.* 2016; Studds *et al.*, 2017), in particular due to habitat loss in localities around Yellow Sea, such as in Saemangeum river estuary in South Korea (Moores *et al.*, 2008). Our analysis does not correspond to these findings since it did not identify any specific flyway or migration strategy as more risky than the others. We suggest that this discrepancy is due to different spatial scales considered because all these previous studies were confined solely to this Asian region, whereas our analysis is global. Therefore, although our result is negative and should be taken with some caution, we find it particularly alarming - it seems that virtually all shorebird migratory systems may be under similar threats as those reported from South-East Asia. This corresponds to recently reported declines of waterbirds in regions with ineffective governance

covering large parts of Latin America, Africa and Asia (Amano *et al.*, 2018) and to declines of Numeniini species spread across different flyways (Pearce-Higgins *et al.*, 2017).

Island endemism showed an unexpected positive relationship to the population increase. This pattern seems counterintuitive at the first glance because population declines would be expected for the restricted-range species which are often threatened at the same time, as indicated by the assessments of IUCN Red List categories (Reif & Štěpánková, 2016; Ducatez *et al.*, 2017). Indeed, island endemics of shorebirds are typically listed as threatened (18 out of 22 island endemic shorebirds in our dataset were listed as threatened or near threatened according to the IUCN Red List) and we found that their threat is a consequence of biotic interactions, namely the pressure from introduced predators. Therefore, it seems that population increase of island endemics within shorebirds results from conservation success in the case of these species. Species facing the highest risk of extinction are targets of higher amount of conservation effort to prevent their global extirpation (Luther *et al.*, 2016). It was exactly the case for island endemics of shorebirds, where the most threatened species enjoyed targeted conservation actions resulting in improvement of their population trends (del Hoyo *et al.*, 2016). Examples of the successful outcomes of the conservation measures applied exist for several species such as Chatham Oystercatcher (*Haematopus chathamensis*), Black Stilt (*Himantopus novaezelandiae*) and Shore Plover (*Thiornis novaezelandiae*) (Dowding & Murphy, 2001; Moore & Reid, 2009; Hagen *et al.*, 2011; Dowding & O'Connor, 2013). Despite a continuing risk from the side of predators and partly also due to direct human persecution, our analysis indicates that these examples actually turned into the global-scale pattern across all shorebirds.

Relationship of the population trend to the number of scientific studies mirrored the level of interest of the global scientific community. We found that declining species and species migrating for longer distances were more often subjected to scientific studies. This result can be viewed as a positive signal of a greater attention towards the species that need it more. Because effective conservation is impossible without a firm scientific background ('evidence-based conservation' *sensu* Sutherland *et al.*, 2015), we can expect that this attention will lead to the improvement of population status of the target species. However, the level of scientific interest may be also shaped by other factors as we found that species with longer generations were more frequently studied. Since generation time is positively correlated with shorebirds' body size (see Methods section), it seems that scientists focus on larger species perhaps due to their higher attractiveness, and not due to their declines. Indeed, a recent study conducted across all vertebrates showed that the research effort was higher towards less threatened species (Ducatez & Shine 2017). Therefore, scientific interest *per se* does not guarantee effective conservation. It is also indicated by our result that the proportion of studies focused on shorebird conservation was unrelated to population trends and any of species' traits.

Conservation implications

Our results provide several important messages for shorebird conservation. (i) It is necessary to focus effort towards long-distance migratory species. Since they are threatened by climate change, it is important to support international climatic agreements on the prevention of further progress of global warming which should in principle result in reducing its impacts.

(ii) Although previous studies confined to regional-level showed particular declines of species using the East Asian / Australasian flyway due to extensive destruction of coastal areas, our global analysis did not support this pattern indicating that the declines of migratory shorebirds are rather widespread and not confided to a specific region. This result implies that a deterioration observed in South-Eastern Asia may be the case also of other migratory and wintering grounds. Although effective conservation might be challenging in these areas, we suggest that increasing pressure from the international conservation community would help to facilitate local conservation actions such as law enforcement in existing protected areas. (iii) Although habitat deterioration was identified among the important threats, we failed to find its link to any of particular habitat types used by shorebirds. Therefore, we cannot recommend that some specific habitats should be better covered by protected areas to deliver conservation benefits to shorebirds. (iv) Instead, population declines were associated with fast life history strategies, namely short generation time indicating that this trait makes species more vulnerable to recent environmental changes. Therefore, we recommend focusing conservation effort at the species level by identifying and eventually protecting the key breeding and non-breeding areas used by the declining species. (v) We found that populations of island endemic shorebirds increased globally, although they are still exposed to threat by biotic interactions (mainly from introduced predators) and are thus listed as threatened. This indicates that the effort invested into their conservation was effective but should be maintained at least until delisting. The example of island endemics also provides a generally positive message for the conservation community that the effort may pay off and that it is possible to reverse the trends and secure the future of the species that we report as currently declining.

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Figures and tables

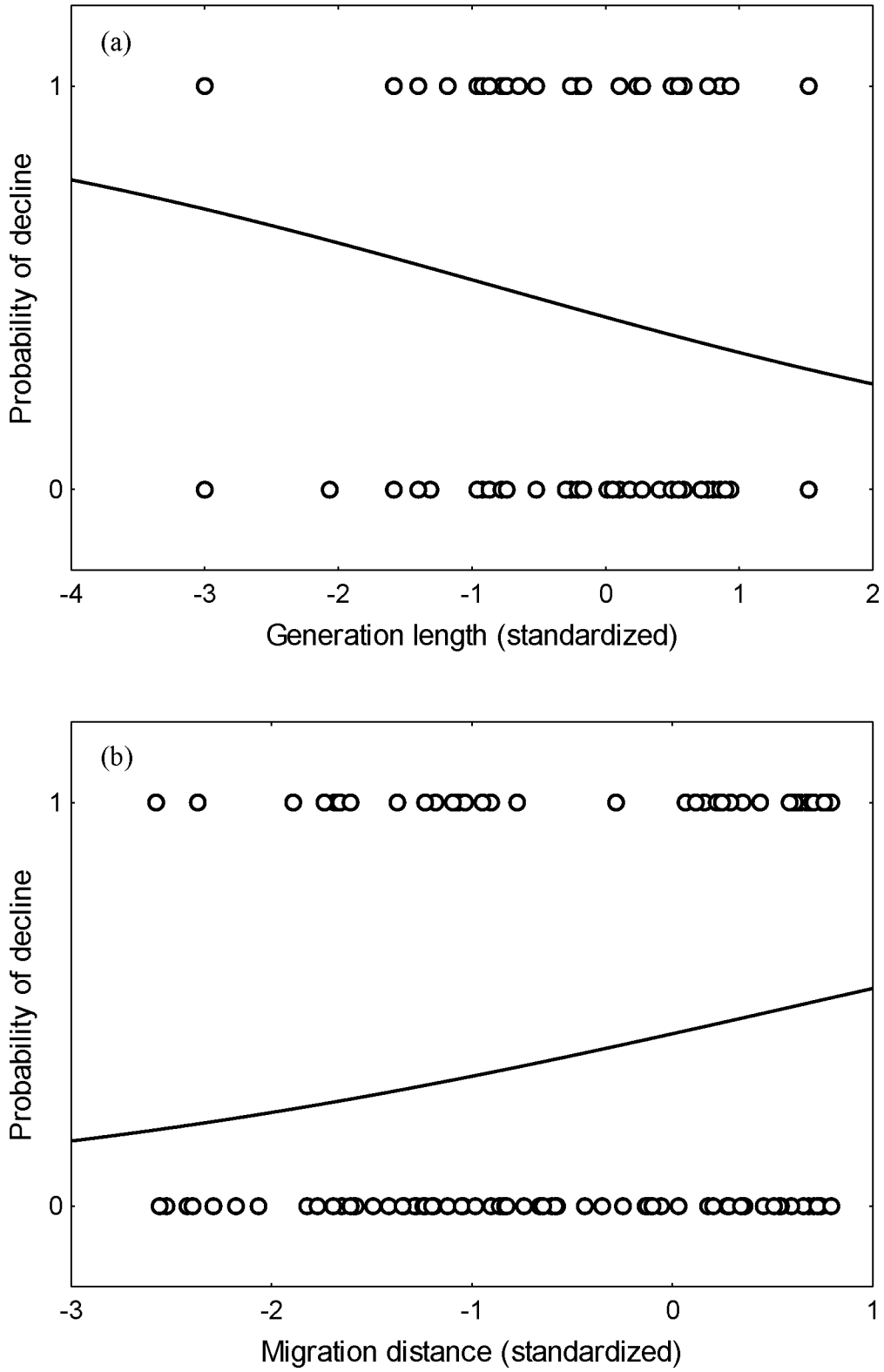

Fig. 1: Relationships between shorebird global population declines and (a) generation time and (b) migration distance, respectively, estimated by generalized linear models with a binomial error distribution and logit link-function. Values of the explanatory variables were standardized to zero mean and unit variance.

Table 1: Relationships between shorebird population declines and species' traits estimated by generalized linear mixed-effects models. (a) Characteristics of the best performing models according to the Akaike Information Criterion ($\Delta AIC_c < 2$). (b) Parameter estimates obtained by averaging across the best performing models. Variables with 95% confidence intervals of their parameter estimates not overlapping zero are in bold. See the Methods section for exact definitions of particular variables.

a)

Model terms	k[a]	AIC_c	ΔAIC_c	model weight
Generation time + migration distance	3	245.6	0.00	0.176
Generation time + migration distance + habitat openness	4	246.1	0.52	0.136
Generation time + migration distance + habitat aridity	4	247.5	1.98	0.066

[a] number of model parameters

b)

Variable	Coefficient	Lower CL[a]	Upper CL[a]
Generation time	**-0.38**	**-0.70**	**-0.06**
Migration distance	**0.46**	**0.13**	**0.78**
Habitat openness	0.20	-0.11	0.51
Habitat aridity	-0.06	-0.36	0.25

[a] confidence limit

Table 2: Relationships between shorebird population declines and species' threats and conservation concerns estimated by generalized linear mixed-effects models. (a) Characteristics of the best performing models according to the Akaike Information Criterion ($\Delta AIC_c < 2$). (b) Parameter estimates obtained by averaging across the best performing models. Variables with 95% confidence intervals of their parameter estimates not overlapping zero are in bold. See the Methods section for exact definitions of particular variables.

a)

Model terms	k[a]	AIC_c	ΔAIC_c	model weight
Habitat deterioration + climate change + direct human persecution + no of scientific studies	5	224.4	0.00	0.290
Habitat deterioration + climate change + direct human persecution + no of scientific studies + proportion of conservation studies	6	225.7	1.28	0.153
Habitat deterioration + climate change + direct human persecution + biotic interactions + no of scientific studies	6	226.1	1.62	0.129

[a] number of model parameters

b)

Variable	Coefficient	Lower CL[a]	Upper CL[a]
Habitat deterioration	**0.63**	**0.27**	**0.98**
Climate change	**0.42**	**0.03**	**0.81**
Direct human persecution	**0.42**	**0.06**	**0.79**
Biotic interactions	-0.14	-0.49	0.22
No of scientific studies	**0.80**	**0.03**	**1.57**
Proportion of conservation studies	0.16	-0.16	0.49

[a] confidence limit

Table 3: Relationships between migratory shorebird population declines and their traits estimated by generalized linear mixed-effects models. (a) Characteristics of the best performing models according to the Akaike Information Criterion ($\Delta AIC_c < 2$). (b) Parameter estimates obtained by averaging across the best performing models. See the Methods section for exact definitions of particular variables.

a)

Model terms	k[a]	AIC_c	ΔAIC_c	model weight
(intercept only)	1	124.1	0.00	0.026
Migration strategy[b]	2	124.2	0.05	0.026
West Asia / East Africa flyway + migration strategy[b]	3	124.5	0.42	0.021
East Atlantic flyway + migration strategy[b]	3	124.8	0.71	0.019
East Atlantic flyway	2	124.9	0.82	0.017
West Asia / East Africa flyway	2	125.1	0.97	0.016
Mississippi Americas flyway	2	125.2	1.07	0.015
Pacific Americas flyway + migration strategy[b]	3	125.3	1.21	0.014
Atlantic Americas flyway + migration strategy[b]	3	125.4	1.28	0.014
Mississippi Americas flyway + migration strategy[b]	3	125.6	1.48	0.013
Atlantic Americas flyway	2	125.7	1.61	0.012
Pacific Americas flyway	2	125.9	1.81	0.011

[a] number of model parameters

[b] distinction between coastal migrant (1), inland migrants (0) and species showing both strategies (0.5)

b)

Variable	Coefficient	Lower CL[a]	Upper CL[a]
Pacific Americas flyway	-0.15	-0.51	0.21
Mississippi America flyway	-0.17	-0.50	0.17
Atlantic Americas flyway	-0.15	-0.49	0.19
East Atlantic flyway	0.22	-0.15	0.58
West Asia / East Africa flyway	0.23	-0.14	0.61
Migration strategy[b]	0.88	-0.28	2.05

[a] confidence limit

[b] distinction between coastal migrant (1), inland migrants (0) and species showing both strategies (0.5)

Table 4: Relationships between shorebird global population increases and species' traits estimated by generalized linear mixed-effects models. (a) Characteristics of the best performing models according to the Akaike Information Criterion ($\Delta AIC_c < 2$). (b) Parameter estimates obtained by averaging across the best performing models. Variable with 95% confidence interval of its parameter estimate not overlapping zero is in bold. See the Methods section for exact definitions of particular variables.

a)

Model terms	k[a]	AIC_c	ΔAIC_c	model weight
Generation time + island endemism	3	117.7	0.00	0.101
Generation time + habitat openness + island endemism	4	117.7	0.02	0.101
Habitat openness + island endemism	3	118.7	1.06	0.060
Generation time + habitat aridity + island endemism	4	119.2	1.56	0.046
island endemism	2	119.2	1.57	0.046
Generation time + habitat openness + artificial habitat + island endemism	5	119.4	1.76	0.042
Generation time + artificial habitat + island endemism	4	119.5	1.83	0.041
Generation time + habitat openness + habitat aridity + island endemism	5	119.6	1.91	0.039
Generation time + migration distance + habitat openness + island endemism	5	119.6	1.99	0.037

[a] number of model parameters

b)

Variable	Coefficient	Lower CL[a]	Upper CL[a]
Generation time	0.47	-0.03	0.97
Migration distance	-0.15	-0.83	0.54
Habitat openness	0.56	-0.22	1.34
Habitat aridity	-0.19	-0.82	0.44
Artificial habitat	0.16	-0.35	0.67
Island endemism	**0.52**	**0.13**	**0.92**

[a] confidence limit

Table 5: Relationships between shorebird population increases and species' threats and conservation concerns estimated by generalized linear mixed-effects models. (a) Characteristics of the best performing models according to the Akaike Information Criterion ($\Delta AIC_c < 2$). (b) Parameter estimates obtained by averaging across the best performing models. Variable with 95% confidence interval of its parameter estimate not overlapping zero is in bold. See the Methods section for exact definitions of particular variables.

a)

Model terms	k[a]	AIC_c	ΔAIC_c	model weight
Habitat deterioration + climate change + direct human persecution + biotic interactions	5	111.0	0.00	0.122
Climate change + direct human persecution + biotic interactions	4	111.9	0.86	0.079
Habitat deterioration + climate change + biotic interactions	4	112.1	1.06	0.072
Habitat deterioration + direct human persecution + biotic interactions	4	112.3	1.28	0.064
Habitat deterioration + climate change + direct human persecution + biotic interactions	6	112.5	1.43	0.059
Direct human persecution + biotic interactions	3	112.7	1.69	0.052
Habitat deterioration + climate change + direct human persecution + biotic interactions + no of scientific studies	6	112.9	1.86	0.048

[a] number of model parameters

b)

Variable	Coefficient	Lower CL[a]	Upper CL[a]
Habitat deterioration	-0.49	-1.05	0.07
Climate change	-4.42	-1221.39	1212.55
Direst human persecution	-0.60	-1.25	0.05
Biotic interactions	**0.82**	**0.34**	**1.31**
No of scientific studies	-0.18	-0.85	0.49
Proportion of conservation studies	0.21	-0.25	0.66

[a] confidence limit

Supplementary Table 1: Dataset used for the analyses containing global population trends and their possible drivers for 184 shorebird species. See Methods section for definition of particular variables.

Supplementary Table 1 is due to its large size placed into a separate excel file which can be downloaded from here: http://www.uschovna.cz/zasilka/BUBZJWW883WCWDHE-2S4/

Supplementary Table 2: Correlation matrix of explanatory variables used for the analysis of shorebird global population trends and their possible drivers. Correlations are expressed as Pearson correlation coefficients. Coefficients higher than 0.70 are in bold.

a) *Species' traits*

Variable	1	2	3	4	5	6
Generation time (1)	--					
Habitat openness (2)	0.18	--				
Habitat aridity (3)	-0.06	-0.16	--			
Artificial habitat (4)	-0.11	0.05	0.20	--		
Migration distance (5)	-0.03	-0.06	-0.07	-0.06	--	
Absolute breeding latitude (6)	0.05	-0.03	-0.18	-0.08	**0.82**	--
Island endemism	-0.05	-0.11	-0.09	-0.03	-0.30	-0.21

b) *Threats and conservation concerns*

Variable	1	2	3	4	5
Habitat deterioration (1)	--				
Climate change (2)	-0.18	--			
Direst human persecution (3)	0.13	0.04	--		
Biotic interactions (4)	0.01	-0.05	0.23	--	
Number of scientific studies (5)	0.08	0.01	0.10	-0.01	--
Proportion of conservation studies	0.09	-0.01	0.11	0.16	0.02

c) *Migratory species*

Variable	1	2	3	4	5	6	7	8	9
Migration strategy (1)	--								
Migratory dispersion (2)	0.16	--							
Pacific Americas flyway (3)	0.27	0.02	--						
Mississippi Americas flyway (4)	-0.13	-0.08	0.61	--					
Atlantic America flyway (5)	0.15	-0.06	0.53	0.68	--				
East Atlantic flyway (6)	-0.05	-0.07	-0.10	-0.20	-0.04	--			
Black Sea / Mediterranean flyway (7)	-0.22	0.02	-0.25	-0.25	-0.24	**0.77**	--		
West Asia / East Africa flyway (8)	-0.17	-0.03	-0.28	-0.28	-0.26	0.69	**0.87**	--	
Central Asia flyway (9)	-0.09	-0.01	-0.23	-0.32	-0.26	0.51	0.56	0.56	--
East Asia / Austral Asia flyway	0.06	-0.04	-0.25	-0.38	-0.32	0.29	0.32	0.23	0.62

Supplementary Table 3: Relationships between shorebird threat from habitat deterioration and species' traits estimated by generalized linear mixed-effects models. (a) Characteristics of the best performing models according to the Akaike Information Criterion ($\Delta AIC_c < 2$). (b) Parameter estimates obtained by averaging across the best performing models. Variable with 95% confidence interval of its parameter estimate not overlapping zero is in bold. See the Methods section for exact definitions of particular variables.

a)

Model terms	k[a]	AIC_c	ΔAIC_c	model weight
Artificial habitat	2	250.7	0.00	0.061
Migration distance + artificial habitat	3	250.9	0.24	0.054
Migration distance	2	251.0	0.27	0.053
(intercept only)	1	251.1	0.38	0.050
Generation time + artificial habitat	3	251.7	1.01	0.037
Generation time + migration distance	3	251.9	1.20	0.033
Generation time + migration distance + artificial habitat	4	251.9	1.21	0.033
Generation time	2	252.0	1.29	0.032
Artificial habitat + island endemism	3	252.0	1.30	0.032
Island endemism	2	252.3	1.59	0.027
Habitat openness + artificial habitat	3	252.5	1.82	0.024
Migration distance + habitat openness + artificial habitat	4	252.6	1.94	0.023
Migration distance + habitat openness	3	252.7	1.99	0.022

[a] number of model parameters

b)

Variable	Coefficient	Lower CL[a]	Upper CL[a]
Generation time	-0.23	-0.60	0.14
Migration distance	0.27	-0.10	0.64
Habitat openness	-0.10	-0.44	0.23
Artificial habitat	0.26	-0.08	0.59
Island endemism	-0.14	-0.45	0.16

[a] confidence limit

Supplementary Table 4: Relationships between shorebird threat from climate change and species' traits estimated by generalized linear mixed-effects models. (a) Characteristics of the best performing models according to the Akaike Information Criterion ($\Delta AIC_c < 2$). (b) Parameter estimates obtained by averaging across the best performing models. Variable with 95% confidence interval of its parameter estimate not overlapping zero is in bold. See the Methods section for exact definitions of particular variables.

a)

Model terms	k[a]	AIC_c	ΔAIC_c	model weight
Migration distance	2	105.5	0.00	0.144
Generation time + migration distance	3	106.9	1.39	0.072
Migration distance + artificial habitat	3	107.3	1.85	0.057
Migration distance + habitat openness	3	107.4	1.90	0.056

[a] number of model parameters

b)

Variable	Coefficient	Lower CL[a]	Upper CL[a]
Generation time	-0.27	-0.94	0.39
Migration distance	**0.54**	**0.05**	**1.03**
Habitat openness	0.12	-0.45	0.70
Artificial habitat	-0.17	-0.77	0.43

[a] confidence limit

Supplementary Table 5: Relationships between shorebird threat from direct human persecution and species' traits estimated by generalized linear mixed-effects models. (a) Characteristics of the best performing models according to the Akaike Information Criterion ($\Delta AIC_c < 2$). (b) Parameter estimates obtained by averaging across the best performing models. Variable with 95% confidence interval of its parameter estimate not overlapping zero is in bold. See the Methods section for exact definitions of particular variables.

a)

Model terms	k[a]	AIC_c	ΔAIC_c	model weight
Generation time + artificial habitat + island endemism	4	235.1	0.00	0.118
Generation time + island endemism	3	235.5	0.39	0.097
Generation time + artificial habitat	3	236.6	1.47	0.056
Generation time	2	236.7	1.59	0.053
Generation time + habitat aridity + artificial habitat + island endemism	5	237.1	1.95	0.044

[a] number of model parameters

b)

Variable	Coefficient	Lower CL[a]	Upper CL[a]
Generation time	**0.37**	**0.05**	**0.68**
Habitat aridity	-0.07	-0.40	0.25
Artificial habitat	0.25	-0.06	0.56
Island endemism	0.29	-0.01	0.59

[a] confidence limit

Supplementary Table 6: Relationships between shorebird threat from biotic interactions and species' traits estimated by generalized linear mixed-effects models. (a) Characteristics of the best performing models according to the Akaike Information Criterion ($\Delta AIC_c < 2$). (b) Parameter estimates obtained by averaging across the best performing models. Variables with 95% confidence intervals of their parameter estimate not overlapping zero are in bold. See the Methods section for exact definitions of particular variables.

a)

Model terms	k[a]	AIC_c	ΔAIC_c	model weight
Generation time + habitat aridity + artificial habitat + island endemism	5	161.2	0.00	0.090
Artificial habitat + habitat aridity + island endemism	4	161.2	0.03	0.088
Artificial habitat + island endemism	3	161.8	0.63	0.066
Generation time + habitat openness + artificial habitat + island endemism	5	161.9	0.71	0.063
Generation time + artificial habitat + island endemism	4	161.9	0.72	0.063
Generation time + habitat openness + habitat aridity + artificial habitat + island endemism	6	162.1	0.94	0.056
Habitat openness + artificial habitat + island endemism	4	162.4	1.28	0.047
Habitat openness + habitat aridity + artificial habitat + island endemism	5	162.6	1.44	0.044
Generation time + migration distance + habitat aridity + artificial habitat + island endemism	6	162.6	1.49	0.043
Migration distance + habitat aridity + artificial habitat + island endemism	5	162.8	1.62	0.040

[a] number of model parameters

b)

Variable	Coefficient	Lower CL[a]	Upper CL[a]
Generation time	0.37	-0.10	0.85
Migration distance	-0.26	-0.87	0.34
Habitat openness	-0.28	-0.75	0.19
Habitat aridity	0.36	-0.08	0.80
Artificial habitat	**-0.53**	**-1.05**	**-0.02**
Island endemism	**0.79**	**0.43**	**1.14**

[a] confidence limit

Supplementary Table 7: Relationships between the number of scientific studies focusing on shorebird species and species' traits estimated by generalized linear mixed-effects models. (a) Characteristics of the best performing models according to the Akaike Information Criterion ($\Delta AIC_c < 2$). (b) Parameter estimates obtained by averaging across the best performing models. Variables with 95% confidence intervals of their parameter estimate not overlapping zero are in bold. See the Methods section for exact definitions of particular variables.

a)

Model terms	k[a]	AIC_c	ΔAIC_c	model weight
Generation time + migration distance	3	521.6	0.00	0.307
Migration distance	2	522.0	0.41	0.250

[a] number of model parameters

b)

Variable	Coefficient	Lower CL[a]	Upper CL[a]
Generation time	**0.17**	**0.04**	**0.31**
Migration distance	**0.28**	**0.14**	**0.42**

[a] confidence limit

Great Knot (*Calidris tenuirostris*) with his clutch and a view over the Pacific, Chukotka, Russia, 2015

Chapter 13

Synthesis and future perspectives

Vojtěch Kubelka

SYNTHESIS AND FUTURE PERSPECTIVES

This thesis comprises an array of studies investigating causes and consequences of predation for breeding shorebirds, together with implications for population dynamics and appealing on conservationists and policymakers. The chapters presented here differ in terms of the scale and scope of scientific impact.

First, many chapters represent regional, often species specific contributions to the large scientific mosaics, improving our knowledge in well-established research and conservation areas. While investigating nest lining size variability in Northern Lapwing (*Vanellus vanellus*), **Chapter 2** supports the thermoregulatory hypothesis but refused the anti-predatory one; it contributes to the long-standing debate on the trade-off between nest size thermoregulatory function and conspicuousness for predators at the same time (Ricklefs, 1983; Deeming & Reynolds, 2015). **Chapter 3** reviews our knowledge on factors influencing the egg size variability, concluding that the seasonal decline in egg size (first vs. replacement clutches) is the most important from tested variables. Together with more food for chicks available at the beginning of hatching season, it represents double advantage for chicks hatched from bigger eggs earlier in the breeding season, which has direct implication for conservation practice. **Chapter 4** presents a finely tuned solution for how to effectively mark nests against agriculture machinery but not attract predators at the same time (Zámečník *et al.*, 2018), which is important for future usage of this conservation measure. This finding contributes to "evidence-based conservation" (Sutherland *et al.*, 2015). **Chapter 5** discusses the newly launched Czech agri-environmental scheme for Northern Lapwing on arable land, effectively promoting the whole biodiversity of the agricultural landscape, similar to recent findings of Schmidt *et al.* (2017). **Chapters 7** and **8** highlight the importance of anti-predatory umbrella effect of active nest defenders for timid species precipitating into the whole marshland bird community species composition, richness and abundance. On the contrary, **Chapter 9** questioned the effectiveness of terns and shorebirds breeding associations and reported high nest predation rates from Caspian Lake region. All these findings contribute to our understanding of interspecific breeding associations importance (Haemig, 2001; Quinn & Ueta, 2008; Sládeček *et al.*, 2014).

Second, two chapters review peculiarities from shorebird breeding and foraging ecology. **Chapter 6** focuses on inter-specific nest scrape reuse among shorebirds concluding that this behaviour occurs more often in rich shorebird communities where more species breeds together and that anti-predatory "protective umbrella" effect can play a role as well (Kubelka *et al.*, 2014). **Chapter 10** describes situations when one shorebird purposefully predates on eggs or chicks of other shorebirds. Despite the fact that majority of these particular inter- and even intraspecific relationships have occurred only once, Ruddy Turnstone (*Arenaria interpres*), Bristle-thighed Curlew (*Numenius tahitiensis*) and both Sheathbills (Chionidae) are regularly effective bird eggs predators. This review extends our knowledge on foraging strategies of shorebirds (Colwell, 2010) and it is outlined for the feedback of International Wader Study Group community before being published, because some more predation events among shorebirds may be hidden in the field notebooks of shorebird researches.

Third, the last section of this dissertation consists of ground-breaking studies, filling major scientific knowledge gaps and shedding light on new research avenues. Three principal implications can be derived from **Chapter 11**: i) For the first time demonstrated historical existence of the global latitudinal gradient in nest predation with higher rates of predation in tropics in comparison with temperate and polar regions, which is the confirmation of long-standing assumption about latitudinal differences in bird nest predation (Skutch, 1949; Ricklefs, 1969; Stutchbury & Morton, 2001); ii) Temporal increase of nest predation is predicted by the extent of climate change at particular breeding sites suggesting the climate-induced alterations of trophic interactions at a global scale; iii) The rapid increase of nest predation in the Arctic, nowadays tripling the historic daily nest predation rates, renders the Arctic no longer the advantageous place to migrate for breeding (McKinnon *et al.*, 2010). On the contrary, the Arctic now represents an extensive ecological trap (Schlaepfer *et al.*, 2002) for migratory shorebirds from nest predation perspective with forecasted negative impacts on their population dynamics. **Chapter 12** further reveals that the longer migration distance of a species, the more likely is the species globally declining. Moreover, migrants' declines are not associated with any specific flyway or migration strategy indicating that not only East Asian-Australian flyway (Piersma et al., 2016) but all flyways may be at risk recently. On the other hand, a positive message can be taken from the revealed link between population increases and island endemism suggesting a success of conservation actions in these species despite the threat from introduced predators. All these fundamental discoveries represent clear messages for conservationists and policymakers and they are provoking future research in following directions.

Species range limitation by predation?

Predation is recognized as factor limiting species ranges (Holt & Barfield, 2009; Sexton *et al.*, 2009; Holt *et al.*, 2011) and predation pressure on bird nests is higher in the tropics than in temperate and polar regions (e.g. Skutch, 1949; Ricklefs, 1969; Stutchbury & Morton, 2001, **Chapter 11**). Therefore one could hypothesize that the edge of a species' range closer to the Equator could be limited by predation. Indeed, M. W. Pienkowski found a gradient in nest predation across breeding range of Common Ringed Plover (*Charadrius hiaticula*) with the highest nest predation in the South, where predation in North-East England was so intensive that author proposed the predation as a factor limiting breeding distribution of Common Ringed Plover from the South (Pienkowski, 1984). Heavy nest depredation was also found at the southern edge of the breeding range for Temminck's Stint (*Calidris temminckii*) in central Finland (Rönkä *et al.*, 2006), however, comparative analysis of this phenomenon is lacking.

Here, I have used population nest predation data collated for **Chapter 11** to provide the first insight into this issue. I test whether populations of the same shorebird species closer to the Equator experience higher nest predation rates than more distant populations. Owing to the recent significant increase of nest predation in North temperate and particularly in the Arctic (**Chapter 11**), I have further excluded data from these regions after the year 2000 for better comparability of studies carried out in different periods. Altogether, I have obtained latitudinal slopes in nest predation for 36 shorebird species with two and more populations per species.

In 22 species (61.1%), the latitudinal slope in nest predation is in concordance with our assumption – with higher nest predation closer to the Equator and 14 species (38.%) shows the opposite trend. The example is given for Northern Lapwing (*Vanellus vanellus*), species with the highest number of populations (Fig. 1). When treating both hemispheres separately, in the South, 75.0% of species (n = 8) follows the proposed pattern, whereas only 57.1% (n = 28) in the North. Despite the dominance of species supporting range limitation by predation, especially in the South, a more detailed investigation is needed. It is necessary to account for the exact slope, the length of the covered latitudinal gradient, the number of populations involved per species and the number of nests per population. It would be interesting to see, whether there are any differences among main shorebirds clades or variance given by body size or level of species aggressiveness to potential predators. Only if the species latitudinal slopes of the nest predation are steeper than the mean latitudinal gradient in the nest predation from all involved populations of all species, than we can assume that predation range limitation play a role and that from life-history perspective, every shorebird species may be adjusted to the particular latitudinal area with local predators by a set of suitable anti-predatory strategies.

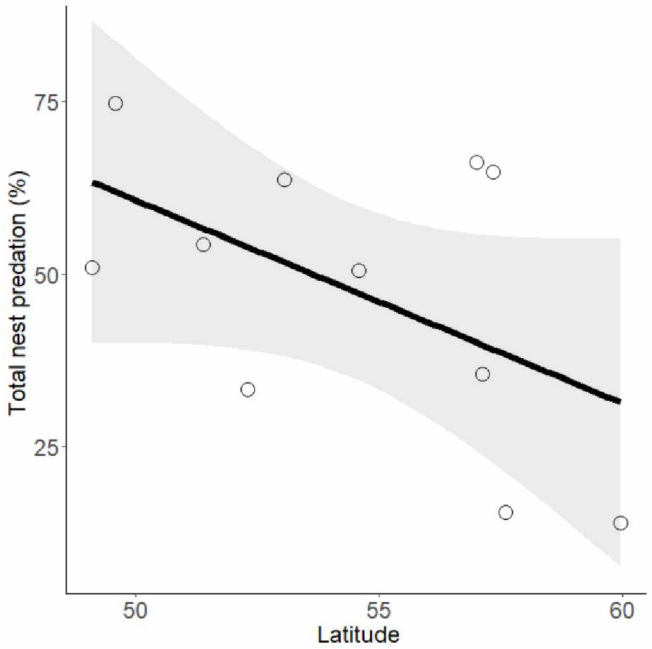

Figure 1. Latitudinal trend in total nest predation for Northern Lapwing. Data from 11 populations of Northern Lapwing (*Vanellus vanellus*) ranging from the Czech Republic to Sweden between years 1974–1999 are included, see details in **Chapter 11**. Regression line together with default 95% confidence intervals from "ggplot" (Wickham, 2009) is presented. These data points represent the most easily available data for Northern Lapwing collected for the purpose of global analysis (**Chapter 11**). It should be possible to obtain at least twice as much data for thorough investigation of this pattern in Northern Lapwing. It is interesting to note that after 2000, some data points could nicely fit into the pattern, as is the case of Austria, latitude 47°N, with 89% total nest predation (Puchta *et al.*, 2009), but note recently low nest predation rates in northern Morocco, latitude 35°N (Cherkaoui & Hanane, 2011).

Small clutch size in the tropics as an anti-predatory strategy?

The future challenge lies in disentangling how much nest predation contributes to the overall mortality and influences trends of shorebird on population level from a comparative perspective. On the species level, it would be interesting to know whether tropical species are able to compensate for high nest predation rate by longer breeding period and more nest attempts. To preliminary address this issue, together with the idea of reduced clutch size in the tropics as an anti-predatory strategy (table 2 in **Chapter 1**), I have prepared a set of figures considering latitudinal variance in reproductive investment among shorebird species (Fig. 2). In line with previous studies (Maclean, 1972; Walters, 1984; Thomas *et al.*, 2007; Colwell, 2010), mean clutch size of shorebirds is on average really somewhat smaller in the tropic (Fig. 2a). Despite a possible reduction of nest predation risk per nesting attempt by smaller clutch size (Arnold, 1999), the number of breeding attempts per year in tropical shorebirds (Fig. 2c) is not high enough to meaningfully elevate the mean number of eggs produced per female per year in comparison with temperate regions (Fig. 2d). Therefore, in light of high nest predation rates in the tropics (**Chapter 11**), smaller clutch size could be partially perceived as an anti-predator strategy (Lima, 1987; Arnold, 1999) but is unlikely that tropical shorebirds could balance high nest predation losses by increased reproductive effort. However, a thorough examination of this issue will need proper testing and correct phylogenetic correction. The further decline of mean clutch size in South temperate and polar regions (Fig. 2a) could be caused by the concentrated presence of shorebird species feeding their young (Ens & Underhill, 2014; del Hoyo *et al.*, 2018), but also this phenomenon would deserve closer investigation.

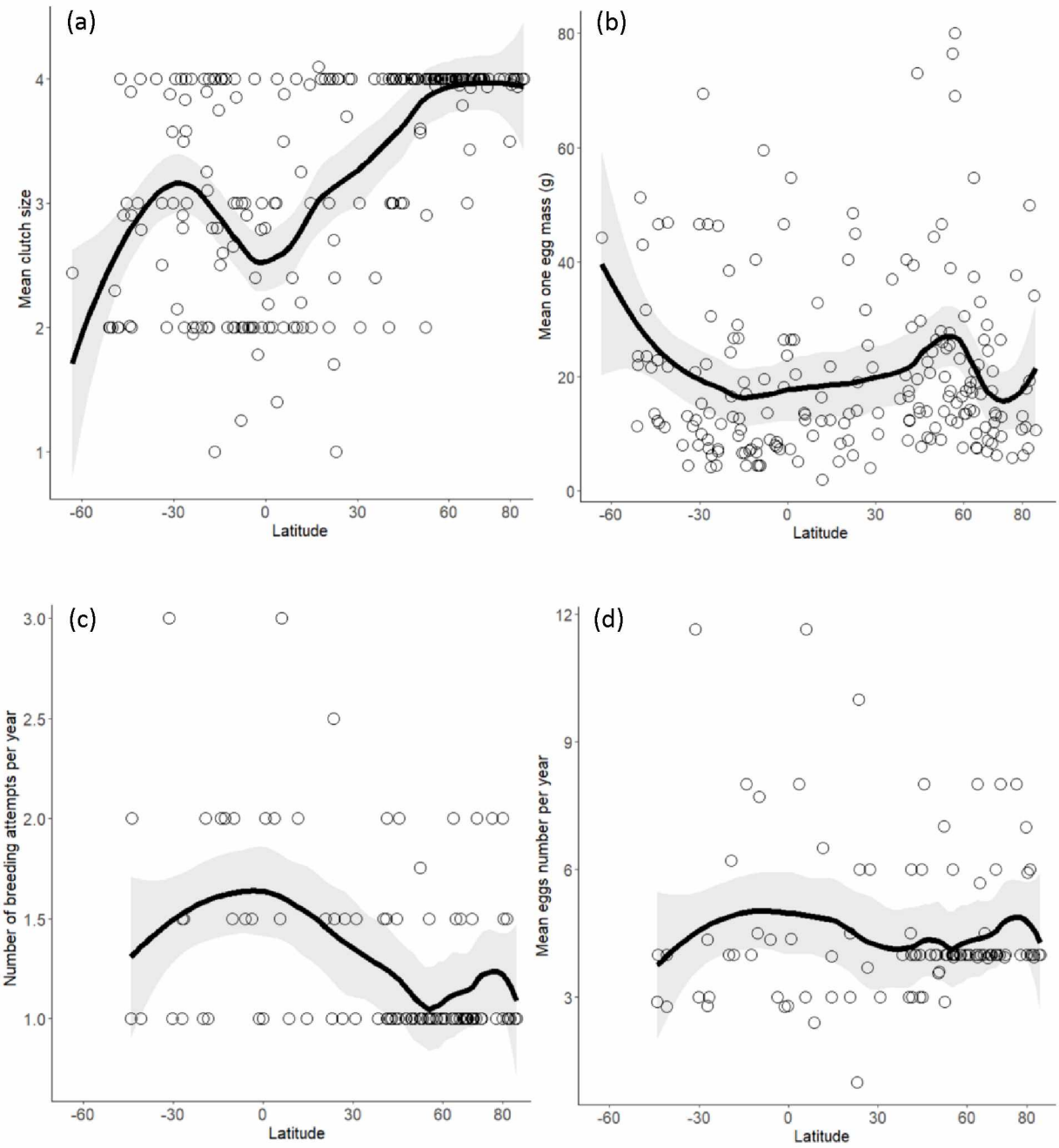

Figure 2. **Reproductive investment of shorebirds in relation to latitude.** Regression curves (loess, span = 0.4) together with default 95% confidence intervals from "ggplot" (Wickham, 2009) are presented. **(a)** Mean clutch size, n = 227 shorebird species. **(b)** Mean egg mass of one egg, n = 208 shorebird species. **(c)** Mean number of breeding attempts per year, n = 111 shorebird species. **(d)** Mean number of eggs laid by female per year, n = 111 shorebird species. Life-history data was adapted from (Myhrvold *et al.*, 2015) complemented with new findings. Note that we still do not know mean number of breeding attempts per year for more than half of all shorebird species. Mean breeding latitude for each species was derived from (BirdLife International, 2018), described in **Chapter 12**.

Biparental care reducing nest predation?

Relating life-history traits and different behavioural anti-predatory tactics to average species nest predation would considerably improve our understanding of anti-predatory strategy evolution, with direct implications for behavioural ecology, comparative demography and species conservation. As an example, we can look at the parental care and address the efficiency of biparental incubation care and mate guarding as a proposed anti-predatory strategy (table 2 in **Chapter 1**). Indeed, in line with expectations, species with predominant biparental incubation care experience on average significantly lower daily nest predation than uniparentally incubating shorebirds (LME; $\chi^2 = 10.72$; P = 0.005, random factor: genus; Fig. 3a). Moreover, even within biparentally incubating species, when the off-duty parent stays near the nest and can help with nest protection, it may further reduce nest predation (Fig. 3b).

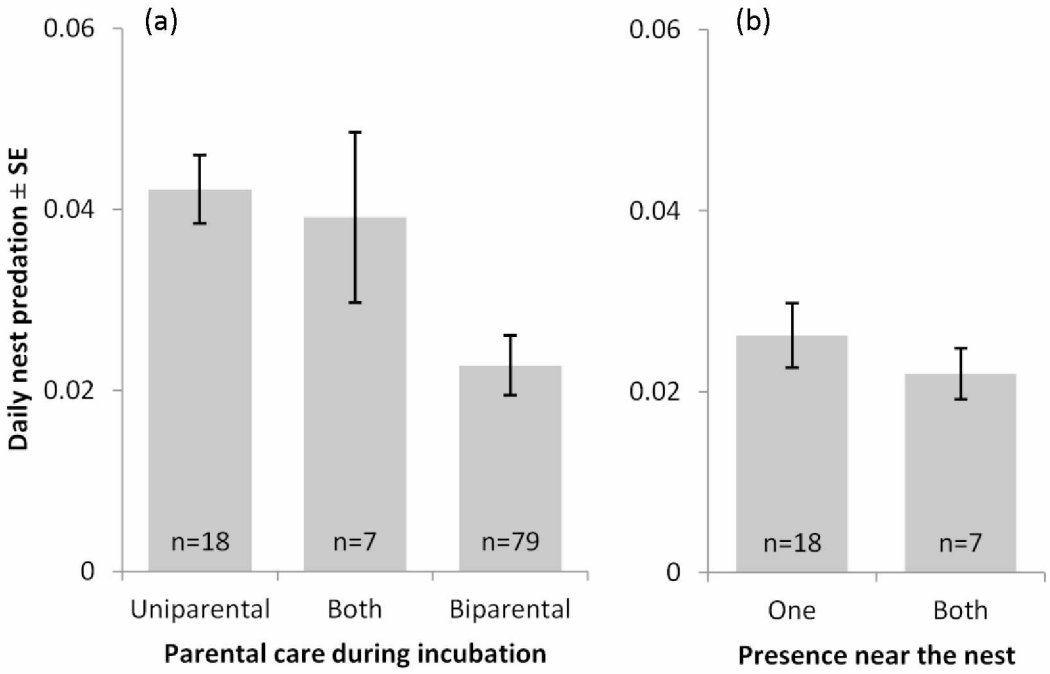

Figure 3. Parental care during incubation in relation to nest predation in shorebirds. (a) Influence of parental care on nest daily predation, n = 104 species. **(b)** Effect of incubating mate guarding within biparental species, n = 25 species. Sample sizes are given in the base of the particular column. Data for nest predation came from **Chapter 11**, data for predominant parental care were adapted from Larsen *et al.* (1996) and complemented with newly available information (del Hoyo *et al.*, 2018). Mean daily nest predation for each species was calculated as the mean from all available population values weighted by the number of nests.

This finding is in line with the fact that the shorter recesses during incubation, the lower nest predation was detected (Smith *et al.*, 2007, 2012) and it generally highlights the importance of anti-predatory strategies involving more individuals (table 2 in **Chapter 1**; Haemig, 2001; Quinn & Ueta, 2008). However, simultaneous evaluation of more behavioural tactics is needed for the complex insight into various anti-predatory strategies effectiveness.

Important role of nest predation in shaping population dynamics?

Chapters 11 and **12** highlight the possible importance of nest predation for the whole population dynamics, however, this direct link has remained untested. I address this issue here with the use of total nest predation rates presented in **Chapter 11** together with BirdLife International global trends and other traits as the mean breeding latitude, habitat loss and generation length, variables introduced in **Chapter 12**, altogether providing information for 213 populations of 94 shorebird species. Total nest predation meaningfully influences population dynamics of shorebirds together with habitat loss and migratory distance (table 1).

Table 1. Significance of factors influencing global decrease or increase in shorebirds. Two models were performed separately treating trends categories binomially as i) decrease vs. stable + increase and ii) increase vs. stable + decrease following the approach used in **Chapter 12**. Generalized linear models with a binomial error distribution and logit link function were used and 213 populations of 94 species included in the analysis. Correlation values among migratory distance, total nest predation and generation length were always smaller than 0.13. Habitat loss was a binomial predictor. Description of the total nest predation variable is given in **Chapter 11**, remaining variables are described in **Chapter 12**.

Model	Decrease vs. stable + increase				Increase vs. stable + decrease			
Variable	Estimate	SE	*z-value*	P-value	Estimate	SE	*z-value*	P-value
Intercept	1.3820	0.783			-0.6581	0.977		
Habitat loss	-1.8870	0.036	-5.24	<0.001	1.5980	0.050	3.17	0.002
Migratory distance	-0.0001	<0.001	-2.78	0.006	0.0003	<0.001	3.75	<0.001
Total nest predation	-0.0015	0.007	-2.18	0.029	0.0254	0.010	2.31	0.021
Generation length	-0.0013	0.075	-0.02	0.986	-0.0325	0.087	-0.37	0.709

The differences in total predation rates are already reflected in global population trends of the shorebirds species. Despite the fact that nest predation is only one part of possible mortalities during the life cycle of bird (Bennett & Owens, 2002), decreasing shorebirds are loosing on average 50.8% of nests to predation whereas species with stable trend 46.1% and increasing species only 35.0% (Fig. 4). This finding confirms the assumption that high nest predation over the longer period (**Chapter 11**) could meaningfully influence global population dynamics (Evans & Pienkowski, 1984; Troy, 1996; Meltofte *et al.*, 2007; Roodbergen *et al.*, 2012). However, in comparison with regional studies (e.g. Troy, 1996; Rönkä *et al.*, 2006; Roodbergen *et al.*, 2012), now the fate of all Holarctic shorebirds is at stake, which has crucial conservation significance and underlines the importance of nest predation as a key factor in avian demography.

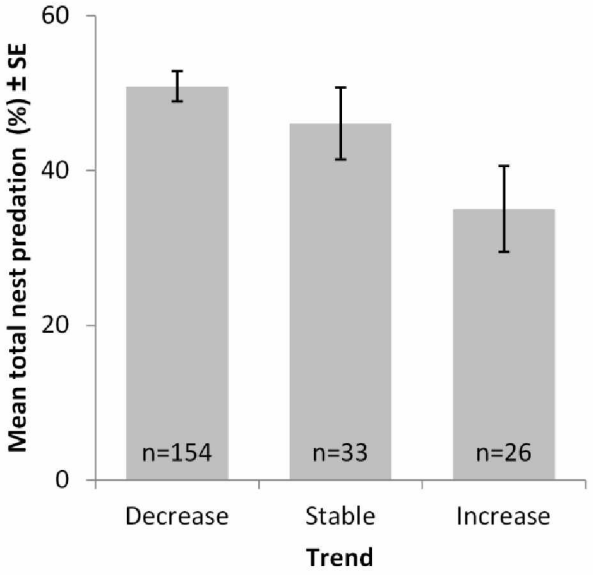

Figure 4. Total nest predation in relation to population dynamics of shorebirds. Sample sizes in the number of populations are given in the base of the particular column. Altogether 213 populations of 94 species with known global trend according to BirdLife International (2018) are included. Description of total nest predation variable is presented in **Chapter 11**.

Through all chapters of this thesis, we have explored links among intrinsic and extrinsic factors influencing nest predation or population dynamics in shorebirds (Fig. 2 in **Chapter 1**). The most fundamental findings of significant relationships are presented in Fig. 5 and can be sum up as follows: Anti-predatory strategies influence nest predation (**Chapters 7** and **8**, but see **Chapter 9**); Latitude and climate change affect nest predation (**Chapter 11**); Life-history traits, namely parental care, influence nest predation (**Chapter 13**); Climate change and life-history traits impact on population dynamics (**Chapter 12**); Nest predation is the significant predictor of population dynamics in shorebirds (**Chapter 13**).

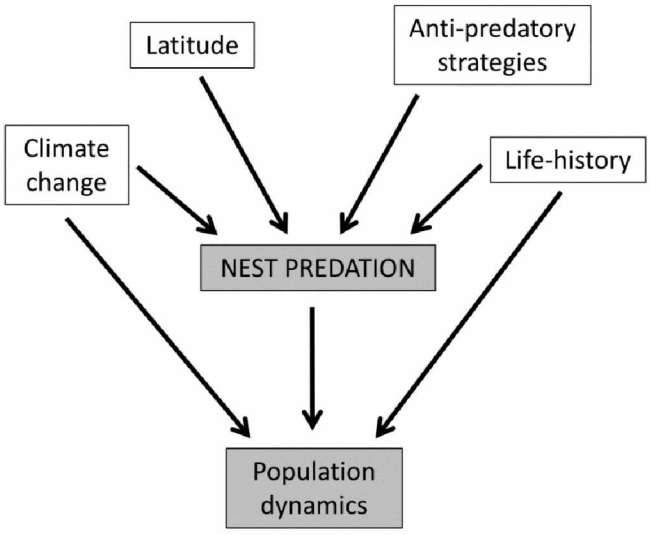

Figure 5. Schematic presentation of the most important relationships confirmed in this thesis.

Future of shorebirds

"Future studies on shorebirds will continue to center on examining breeding behavior and ecology, migration, and foraging behavior. However, more emphasis will be placed on examining the entire life cycle of particular species, comparing the success of populations that differ in breeding sites, breeding and nonbreeding habitats, and migration routes. Finally, the mechanisms that control behavioral and ecological plasticity in shorebirds should provide some of the most interesting avenues for future research."

(Burger & Olla, 1984)

It is strikingly obvious, that the statement which was proposed by Jolana Burger and Bori L. Olla in the introduction to the "*Shorebirds – Breeding behavior and populations*", the ground-breaking publication released in 1984, is still highly relevant 34 years later. Many interesting findings have been made while many more discoveries still wait to be revealed. After more than 20 years (Piersma *et al.*, 1997), there are still persisting huge gaps in our knowledge about tropical and South American shorebirds (**Chapter 11,** Fig. 2), which represents a great challenge for enthusiastic shorebird researches in close future.

What makes the current age markedly different from earlier times, is the fact that shorebirds on average do worse and there are less of them with us today than it was several decades ago. European farmland shorebirds have undergone severe declines (BirdLife International, 2004), mainly due to agricultural intensification and increased predation pressure (Roodbergen *et al.*, 2012). North American migratory shorebird populations have decreased by more than 60% since that time, as a result of habitat loss and degradation at the key coastal stopover sites as well due to the influence of climate change (North American Bird Conservation Initiative, 2016). Shorebirds migrating along East Asia-Australasian flyway dropped down a lot in their numbers due to megalomaniacal reclamation projects damaging vast intertidal mudflats, essential staging areas for shorebirds (Piersma et al., 2016; Studds et al., 2017). For example, one analysis suggests that a single big reclamation project in Saemangeum river estuary in South Korea could be responsible for 20% loss of global population in Great Knot (*Calidris tenuirostris*), endangered species breeding in Chukotka (Moores *et al.*, 2008). Of course, there are positive exceptions (e.g. **Chapter 12**), but the general trend is negative.

Globally, out of 192 shorebirds with known species trend (remaining 53 species are classified with unknown trend), 110 species (57.3%) are declining, 60 species (31.2%) are stable and only 22 species (11.5%) were assigned as globally increasing (BirdLife International, 2018; Fig. 6). In line with the fact that shorebirds migrating on longer distances perform even worse (**Chapter 12**), from Fig. 5 is obvious that in Holarctic shorebirds, the decline is the most predominant population trend. On the contrary, all trend categories are evenly represented among South temperate shorebirds (Fig. 5a). The higher percentage of increasing shorebirds there could be a result of effective conservation measures (**Chapter 12**). Generally, Plovers (Charadriidae) perform a somewhat better than Sandpipers (Scolopacidae) (Fig. 5b), however, members of later clade are on average breeding further North (BirdLife

International, 2018), therefore these differences could be determined more by the geographic location of breeding grounds rather than other intrinsic traits of families but differences in population trends among shorebird clades remain to be closely investigated.

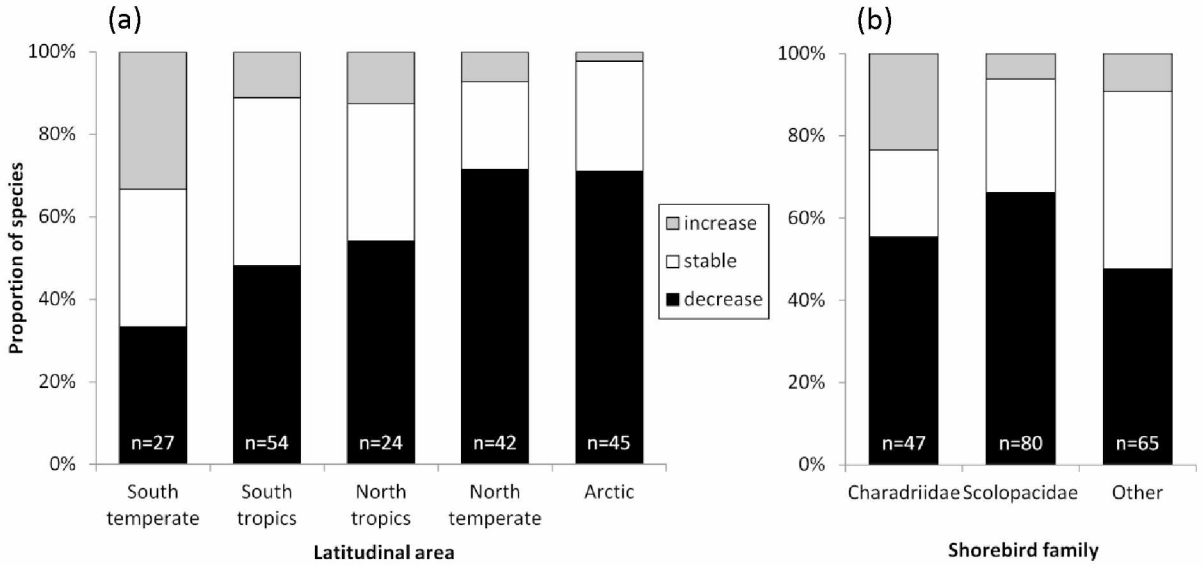

Figure 6. Global population trends of shorebirds. Data divided according to **(a)** Latitudinal areas and **(b)** Shorebird families. Shorebirds were adjusted to the particular area according to mean breeding latitude. Data comes from BirdLife International, (2018). Out of 245 shorebird species (table 1 in **Chapter 1**), altogether 192 species with known global population trend are involved. Sample sizes are given in the base of the particular column.

Currently, migratory shorebirds are squeezed by deteriorating adult survival caused predominantly by the loss of suitable staging areas during migration (Piersma *et al.*, 2016; Studds *et al.*, 2017; Weiser *et al.*, 2018), and climate change induced poor reproductive output, generated by recently excessively high nest predation in northern breeding grounds (**Chapter 11**), a trophic mismatch during chick-rearing period (Gilg *et al.*, 2012; van Gils *et al.*, 2016) and predicted shrinkage of suitable breeding habitat (Meltofte *et al.*, 2007; Gilg *et al.*, 2012). Climate change effects on shorebird populations are expected to get pronounced (Meltofte *et al.*, 2007; Galbraith *et al.*, 2014), which inevitably imply a further global decline of migratory shorebirds.

As shorebirds enthusiasts, we are responsible for the fate of shorebirds and conservation should matter to us. It is difficult to directly mitigate large-scale impacts of climate change, but every little helps – from one nest direct protection to setting up large national reserves preventing habitat loss or promoting international cooperation in shorebirds and their habitat conservation. As scientists, we should take our time to disseminate our results among conservationists and policymakers, as well as we should translate our finding for the wider public. Our work does not end by publication and our voices about shorebird problems must be heard, because general public awareness is the key for turning scientific knowledge into effective conservation. Shorebirds deserve our attention from the conservation perspective, especially now, during the era of rapid changes in the global environment (Tylianakis *et al.*, 2008; Gilg *et al.*, 2012; Scheffers *et al.*, 2016).

Taken together, we have witnessed that shorebirds really represent the very special group of birds per se, unique in many aspects of breeding ecology and their very diverse life-history strategies. Moreover, shorebirds are the suitable model group for not only testing evolutionary theories of life histories, sexual selection and adaptation, but they are also excellent environmental indicators from the conservation perspective. However, shorebirds are declining globally and we still not fully understand to factors limiting their populations. Therefore now, more then ever, the disentangling and relevance assessment of particular factors driving population dynamics of shorebirds at individual populations scale but from the worldwide comparative perspective with direct precipitation into conservation practice is urgently needed to secure future for our admirable shorebirds.

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Spoon-billed Sandpiper (*Calidris pygmaes*) at Chukotka breedig ground, Russia, 2010 and 2015